2005

Community-level effects of solar ultraviolet radiation on benthic marine assemblages in Antarctica and Australia

Jeffrey L. Kinley
University of Wollongong

Community-Level Effects of Solar Ultraviolet Radiation on Benthic Marine Assemblages in Antarctica and Australia

Jeffrey L Kinley Jr

A thesis submitted in partial fulfillment of the requirements for the award of the degree of Masters by Research (Biological Sciences).

University of Wollongong
March 2005

Declaration

I, Jeffrey L. Kinley Jr, declare that this thesis, submitted in partial fulfillment of the requirements for the award of Masters by Research, in the Department of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

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Jeffrey L Kinley Jr

March 2005

To speak truly, few adult persons can see nature. Most persons do not see the sun. At least they have a very superficial seeing. The sun illuminates only the eye of the man, but shines into the eye and heart of the child. The lover of nature is he whose inward and outward senses are still truly adjusted to each other; who has retained the spirit of infancy even into the era of manhood.

—Ralph Waldo Emerson

They that go down to the sea in ships,
that do business in great waters,
These see the works of the Lord,
and His wonders in the deep.

—Psalm 107

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Abstract

The destruction of the stratospheric ozone layer due to the anthropogenic production of ozone-depleting substances has led to the increased transmission of harmful ultraviolet-B radiation (280-320 nm) to the surface of the earth. Although exposure to ultraviolet radiation (UVR) is shown to be directly harmful to numerous marine species, less is known about the impacts of UVR at the community-level. To investigate the ecological effects of ambient solar UVR on macrobenthic assemblages in shallow-water marine environments, field experiments were used near Casey Station, East Antarctica and Wollonging, NSW, Australia. In both locations, experiments were done in the shallow subtidal zone using experimental panels and UV cut-off filters. To allow for maximum levels of UVR, experiments were done during the Austral summer. To test whether current levels of ambient UVR had any effect on macrobenthic assemblages developed in situ, experimental panels were placed under four different irradiation treatments (no UVR, transmits PAR only; no UVB, transmits PAR + UVA; an acrylic procedural control, transmits PAR + UVA + UVB; and a no-filter control, transmits PAR + UVA + UVB) and later collected for examination in the laboratory. The responses of the assemblages to the various treatments were determined by measuring diversity, total biomass, and community composition. Experimental panels in Antarctica were deployed between January and February 2001. After 46 d in the field, benthic marine diatoms dominated all the panels in all treatments. Up to 77 species of diatom were identified and recorded. Univariate analyses on

species richness and diatom biomass revealed no significant differences among irradiation treatments. Overall, there were no significant impacts of UVR on the community structure of benthic marine diatom assemblages in Antarctica. In Australia, short-term (~19 d) and long-term (84 d) experimental panels were deployed at two locations between January and March 2002. At the end of the experiments, all panels in both locations were dominated by stands of red or green ephemeral algae. While univariate analyses sometimes revealed significant effects of UVR on number of taxa, total biomass, and percent cover of algae, these effects were generally weak and inconsistent. In the few cases, where multivariate analyses detected differences in community structure, UVA often had more of an effect on community structure than UVB. Thus, while it appears that in some cases UVR is capable of influencing shallow-water macrobenthic assemblages, I contend that these effects are relatively subtle and inconsistent. It is therefore concluded that the community-level impacts of UVR on benthic marine assemblages are weak and transient, not pronounced and persistent. This conclusion is primarily based on the notion that in high-irradiance environments, the effects of UVR are likely to be mitigated over time. This could possibly occur through the facilitative effect of a UV-resistant community dominant, which could provide refuge for UV-sensitive species and thereby diminish the impacts of UVR over time. Because of this, temporal scale is going to be a crucial factor in the outcome of any future experiments that address the effects of UVR at the community-level.

Acknowledgments

I would like to thank everyone at the University of Wollongong who helped make this research possible. In particular I would like to acknowledge my supervisor, Dr. Andy Davis. I thank him greatly for giving me the wonderful opportunity to study ecology, not only in Australia, but in Antarctica, as well. I was fortunate to have his trust and faith in my abilities. Thanks also to everyone who contributed comments, suggestions, and criticisms during the final stages of this thesis. This includes, Peter Barnes, Nerida Bleakley, Sharon Robinson, David Ayre, and Rob Whelan.

I acknowledge Dr. Martin Wahl, from the University of Kiel in Germany, as the mastermind of the global UV project. Because of him, Andy and I were able to do research in the Antarctic and to contribute to a unique, global ecological research project. I also acknowledge the expertise of my colleague, Nerida Bleakley, for analyzing the diatom samples from Antarctica and for her contribution to the Methods section of Chapter 2. Special thanks are due to Dr. Sharon Robinson for the use of her spectrometer and UV meter. I pay tribute to Elisabeth Peisley, the Science Faculty Librarian, who sent me important journal articles to Antarctica.

Many thanks to the members of the 54th ANARE for a productive and enjoyable summer at Casey Station. Logistical support was made possible by an exceptional group of "tradies", most notably Paul Saxby, Leon, Sel and Mickey. I would

especially like to thank the boating "boffins", Julian Finn, Bob Edgar, Sarah Richards, and Tom Velthuis for their dedication while helping me in the field. In the lab, Laura Cunningham and Gary Mayo did a great job helping me collect and prepare the diatom samples. Special thanks go to Rupert and Snake, for the intimate experiences with the elephant seals and for time well spent on the "frontier".

I also thank everyone who helped me get through the demanding field season in Wollongong, Australia. Trudy Franks, Peter Barnes, Cary Rodgers, Simone Duerr, Adam "George" Lodding, and Will Glamore all contributed to the work in the field. I am especially grateful to Adrian Ferguson, Rob Hutchings, and Jodi Dunn, who did well and beyond their duty as volunteers. I owe each of them a huge favor.

I would like to thank the Australian Antarctic Divison (AAD) for making the Antarctic research possible. Funding for the Antarctic portion of this research project was provided through ASAC and AAS grants. The research project in Australia was in part funded by the PADI project AWARE micro grant program.

I give thanks to all of my family and friends for their love, guidance, and support during this endeavor. I realize that my adventuresome and unorthodox lifestyle has been, at times, difficult to endure. I thank Bob and Bia Kirchiro, who encouraged me to travel and helped me see beyond borders and nationalities. I thank my brother, Cory Kinley, who always reminds me that hard work and positive thinking will yield success. I thank 'uncle' Bill and Colleen Moore for

their love and generosity. Special thanks go also to my 'aunt', Sharon Seybold, for trusting me and investing in my future.

I am grateful to my parents, Carole & Brian Hunt, and, Jeffrey L Kinley Sr, for their love and patience. No matter what pursuits in life I chose, they were always supportive and allowed me to discover myself freely. I thank my step-father, Brian Hunt, for inspiring me to harness my creative powers and put them to good use on a Macintosh computer. I thank my dad for teaching me how to build and fix things and for always having the time and patience to answer my questions. I am deeply grateful to my mom for helping me discover Mother Ocean and all of Her greatness.

I thank my best buddies, Brian Leach, Mike Colpo, Mark Hughey, and Nathan Tanner, for always being there when I needed them.

The support and encouragement from my partner, Sabine Thier, during the writing of this thesis was greatly appreciated. Making a commitment to live with someone is one thing, but doing so while one has a thesis to write takes cohabitation to a new level. Her patience and understanding during the hard times, gives me hope and inspiration for whatever challenges we may face in the future.

Finally, I thank Dr. Lawrence Curtis, my mentor, my teacher, my friend. He, above all, made this possible for me.

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Chapter 1
General Introduction

And there's a hole in the atmosphere,
gets bigger every time you spray your hair.

—Graham Parker

Introduction

The anthropogenic production of ozone-depleting substances has led to the reduction in stratospheric ozone and the consequent increase of ultraviolet radiation to the surface of the earth (WMO 1999). As a consequence, organisms on earth are at risk of being exposed to above normal levels of biologically harmful ultraviolet-B radiation (UVB). In this thesis, I examined the biological impacts of ultraviolet radiation on hard-bottom, macrobenthic assemblages in both Antarctica and Australia. In order to place the biological aspects of this thesis into context, however, it is first necessary to explain the nature of ultraviolet radiation on earth and discuss the protective role of the stratospheric ozone layer.

The Role of Stratospheric Ozone

Ozone (O_3) is a toxic and chemically-reactive form of molecular oxygen (O_2) that is present in both the troposphere (0–11 km) and in the stratosphere (11–50 km). The stratospheric ozone 'layer' refers to the region of the atmosphere between 15 and 35 km above the earth, where the majority (~90%) of natural ozone occurs. Although it is often described as if it were a dense layer, ozone molecules in this region are actually sparse and diffuse. Indeed, if all the ozone in a column of the stratosphere was heated to 0° C and compressed to a partial pressure of 1 ATM (STP), the ozone would form a layer only 3 mm thick (Christie 2001). In the troposphere, ozone is a harmful, human-based pollutant that contributes to poor air quality and global warming. In the stratosphere, however, ozone occurs naturally and forms a protective barrier that shields life on earth from harmful solar ultraviolet radiation.

The Basic Concepts of UV Photobiology

Ultraviolet radiation (UVR) is a form of short-wave (nanometers), electromagnetic radiation that is emitted from the sun (Figure 1). The majority of solar radiation never makes it to the surface of the earth because it is either reflected or absorbed by gases in the atmosphere (Figure 2). In particular, ozone selectively absorbs harmful short-wave UVC (above 220 nm) and UVB (280–320 nm) radiation, while letting longer wavelengths like UVA (320–400nm) and photosynthetically active radiation (PAR, 400–700 nm) pass through the atmosphere unimpeded.

UVB radiation is usually regarded as the most harmful to organisms, because it is directly absorbed by organic molecules like DNA and proteins (Häder & Worrest 1991). As such, UVB has the capacity to cause cellular damage by altering molecular structure and thereby possibly impairing the function of DNA. Unlike UVB radiation, UVA is not as readily absorbed by DNA and thus does not directly cause significant damage to DNA. However, it is possible for UVA to cause indirect oxidative damage to DNA through photochemical reactions that create peroxide and hydroxyl radicals (Karentz & Bosch 2001). Despite the hazardous potential of UVA exposure, UVA is also implicated in DNA photorepair processes (e.g. photoreactivation) (Karentz 1994; Karentz & Bosch 2001). Thus, depending on the circumstances, UVA can have both harmful or beneficial biological effects on organisms (Karentz 1991).

Stratospheric Ozone Depletion

The anthropogenic production and release of ozone-depleting substances into the atmosphere, most notably chlorofluorocarbons (CFCs), has led to a significant reduction in average global stratospheric ozone levels (Molina & Rowland 1974; McFarland & Kaye 1992). CFCs and other chlorine-based substances destroy ozone by catalyzing the conversion of ozone (O_3) to regular molecular oxygen (O_2). Depletion of the stratospheric ozone layer leads to the increased transmission of ultraviolet-B radiation (UVB, 280-320 nm) to the Earth's surface (Frederick & Snell 1988; Kerr & McElroy 1993; Madronich et al. 1998).

The most widely-known consequence of stratospheric ozone depletion is the Antarctic ozone hole. Due to the combination of unique meteorological conditions and the presence of halocarbons (CFCs and halons) in the atmosphere above Antarctica, springtime (Sept-Nov) ozone losses of more than 50% have occurred annually over the Antarctic continent for over two decades (Staehelin et al. 2001). Evidence of the ozone hole was first discovered in 1985 by a team of scientists working for the British Antarctic Survey who had been monitoring ozone levels at Halley Bay, Antarctica for 28 y (Farman et al. 1985). Their measurements showed a clear seasonal decline in column ozone values from about 1976 to 1984. In contrast, during the years prior to this, from 1957 to 1975, there were no such losses. Later, the measurements recorded by Farman and his colleagues were confirmed by data collected from the Solar Backscatter Ultraviolet (SBUV) instrument and the Total Ozone Mapping Spectrometer (TOMS) aboard NASA's Nimbus-7 satellite (Stolarski et al. 1996). In the years since then, TOMS measurements continue to show the ever-increasing size of the ozone hole over the Antarctic continent and surrounding Southern Ocean (Figure 3). In September 2000, the hole reached an all-time record size of 28.3×10^6 km^2, an area that is three times larger than the United States (Anonymous 2000). While the most severe destruction of the ozone layer has occurred over the Antarctic continent, substantial ozone losses have also occurred at mid-latitudes (WMO 1999; Staehelin et al. 2001).

Attempts to curb the depletion of ozone through treaties such as the Montreal Protocol have been partly successful and the emission of ozone-depleting substances is leveling off, or possibly decreasing. Despite these measures, it appears that total recovery of the ozone may not occur until at least the middle of this century (WMO 1999). Nonetheless, even without ozone depletion, ambient levels of UVB are still harmful to many organisms because UVB can cause direct mutagenic DNA damage (Harm 1980).

Ultraviolet Radiation in the Marine Environment

In a pioneering study more than half a century ago, Jerlov (1950), measured levels of sub-surface UV radiation in the sea and discovered that the photochemically active zone of the world's oceans could extend to 20 m. Despite his findings, a widespread misconception, that UV radiation does not penetrate more than a few meters below the ocean's surface, persisted into the 1980s (Norris 1999). More recently, however, advances in scientific instrumentation have allowed scientists to make more accurate measurements of UVR in aquatic ecosystems. For example, Karentz & Lutze (1990) used a biological dosimeter that detects the presence of UVR by measuring DNA damage in *Escherichia coli*. Their results support Jerlov's initial claims and have confirmed the presence of biologically harmful radiation to depths of 20 to 30 m. In addition, Smith and others (1992), using an ultra-sensitive submersible spectroradiometer, detected UVB radiation at depths beyond 60 to 70 m in the Bellingshauson Sea. Now that there is greater

awareness of the existence of UVR in the ocean, the potential impacts of UVR on organisms in shallow marine environments must be considered.

The Detrimental Effects of UVR in Marine Systems

The detrimental effects of UVB have been documented on a variety of marine organisms such as, ascidians (Bingham & Reyns 1999; Bingham & Reitzel 2000), echinoderms (Giese 1938; Johnsen & Kier 1998), crustaceans (Karanas et al. 1979; Damkaer & Dey 1983; Hovel & Morgan 1999), corals (Gleason & Wellington 1993; Gleason 1993; Gleason & Wellington 1995), and sponges and bryozoans (Jokiel 1980), but these studies examined only species-specific effects. In contrast, examination of the community-level effects of UVR on marine assemblages is limited. Where community-level effects of UV have been studied, there is a focus on microbial phytoplankton communities (Worrest et al. 1978; Davidson et al. 1996; Wängberg et al. 2001; Davidson & Belbin 2002), and less attention given to benthic communities.

While the negative impacts of UVR at the organismal level are well documented (UNEP 1998), less is known about the community-level impacts of UVR. Not all organisms are equally sensitive to UVR because of interspecies differences in defense mechanisms that protect organisms. Thus, it has been suggested that the differential sensitivity of organisms to UVR may lead to changes in community structure. While shifts in community structure have been detected in both marine

and freshwater environments, the overall impacts of UVR in aquatic ecosystems remains ambiguous (Wahl et al. Submitted).

More than 80% of the earth's phyla, the majority of which are invertebrates, are found only in the sea. Because many of these populations exist at depths shallower than 200 m, nearly all of these organisms will at some stage in their lives be influenced by sunlight (Thorson 1964). Recent estimates of the number of benthic marine invertebrate species range from half a million (May 1992) to 5 million (Poore & Wilson 1993) to 10 million species (Grassle & Maciolek 1992). If these organisms are unable to detect the biologically-harmful components of solar radiation they will not be able to respond successfully to increased levels of ultraviolet radiation (UVR) in their environment. Sessile marine invertebrates, in particular, may be vulnerable to UVR because once settled, they cannot move to avoid UVR (Williamson 1995).

Reviews on Ultraviolet Radiation and the Marine Environment

The majority of reviews dealing with UVR and the marine ecosystem have focused on phytoplankton or primary productivity (Worrest 1983; Smith & Baker 1989; Häder & Worrest 1991; Häder et al. 1995). There are two reasons for this emphasis. First, there are concerns that the inhibition of primary productivity will decrease global carbon fixation rates, thus raising global levels of CO_2, which could accelerate global warming trends. Second, negative impacts at the base of the food chain may initiate a cascade of catastrophic effects up through other trophic levels. As mentioned in a number of articles (Häder et al. 1995), it has

been suggested that a 16% reduction in ozone levels may result in a 5% loss in phytoplankton, which—transferred through the food chain—equals a loss of 7 million tons of fish annually. Not all reviews deal exclusively with primary productivity. Other reviews have focused on Antarctic ecology (Voytek 1990; Karentz 1991), marine macroalgae (Franklin & Forster 1997), and the effects of UV on freshwater systems (Williamson 1995).

Direct and Indirect Effects of UVR

Despite tremendous advances in UVR research, little is known about the impacts of UVR at the community level (Worrest 1983; Häder et al. 1995; Williamson 1995). Historically, it appears early attempts to understand the role of UVR in biological systems were from a physiological perspective because they examined only direct effects at the organismal level (Giese 1938; Damkaer et al. 1980, 1981; Damkaer & Dey 1982; Peak & Kubitschek 1982; Damkaer & Dey 1983). In almost every case, experiments were conducted in the lab using artificial radiation. Currently, it appears that research efforts continue to concentrate on the direct effects of UVR in the laboratory (see below), even though it is still unknown how the effects of UVR on one group of organisms may affect wider ecological processes.

One of the problems with this methodological approach is that effects are often species-specific, and, therefore, do not always provide the best indication of impacts occurring on the community as a whole (Keller et al. 1997a). An alternative approach would be to examine the effects of UVR on whole

communities by designing experiments that observe recruitment and colonization patterns of organisms in an assemblage under various treatments (i.e. UVB, UVA, PAR) of natural solar radiation. By carefully monitoring and measuring changes in biomass and species composition it is possible to record not only the direct effects of UVR on the community but indirect effects as well.

Forging a new path in UV research, a number of recent studies have used this approach in both marine (Keller et al. 1997a, b; Odmark et al. 1998; Nozais et al. 1999; Wulff et al. 1999) and freshwater environments (Bothwell et al. 1994; Hill et al. 1997; Kiffney et al. 1997; Vinebrooke & Leavitt 1999). While a couple of these studies have not detected community-level effects of UVR (Hill et al. 1997; Keller et al. 1997b) others have (Bothwell et al. 1994; Santas et al. 1997, 1998a, b; Lotze et al. 2002).

The most notable demonstration of how UV can indirectly affect an aquatic community was reported by Bothwell and others (1994). In this study, Bothwell and his colleagues used three treatments of solar radiation—No UVR (Blocks 280-400 nm), No UVB (Blocks 280-320 nm), and full-spectrum sunlight (280-700 nm)—on algae and grazer (chironomid) communities in a freshwater mesocosm experiment. By monitoring biomass of algae and the grazers under the various treatments, they discovered that algal biomass was greatest under treatments exposed to UVB, not because algae were insensitive to UVB, but because of reduced grazing pressure of the chironomids. In contrast, algal biomass was much lower in the treatments without UVR, where chironomid abundance was

higher and grazing pressure on algae was maintained. The outcome of this study demonstrates that it may be difficult, if not impossible, to make predictions about ecosystem-level responses to UVR based on only one trophic level. As Williamson (1995) has suggested about freshwater ecosystems, "complex rather than simple responses [to UV-B] are likely to be the rule".

Laboratory Versus Field Studies

Most of our knowledge about UVR and marine invertebrates in temperate regions is from laboratory studies. A survey of articles published on the effects of UVR on marine invertebrates revealed that 42% of 45 experiments were conducted in the lab in temperate regions. In contrast, field studies in temperate regions constituted only 20% of these 45 publications. This is not to say that laboratory studies are irrelevant; they are not. Like any type of study, they have their advantages and can be used effectively to elucidate important information (Diamond 1986). There are concerns, however, that the disproportionate number of laboratory versus field studies may be limiting our understanding of the real impacts of UVR in natural environments.

One caveat for conducting UVR experiments in the laboratory is the use of artificial UVR. Often artificial UV originates from a fixed source, so that fluence rate and spectral properties are constant; however, in natural systems solar radiation fluctuates and the distribution of wavelengths is perpetually changing in response to environmental factors that influence the intensity of solar radiation (Karentz & Lutze 1990). Also, inaccurate representations of solar radiation can

occur when the components of simulated solar radiation are absent or exaggerated. In short, it is difficult to duplicate the high variability of natural UVR in laboratory settings (Worrest 1983; Bingham & Reitzel 2000). Unfortunately, this may lead to problems when extrapolating laboratory results.

First, care must be taken when extrapolating laboratory results into the natural environment (Smith & Baker 1989; Worrest 1983). For example, Bingham & Reyns (1999) conducted a laboratory study examining the effects of artificial UV on the life history stages of *Corella inflata*, a solitary ascidian endemic to Washington, USA. While they incorporated a 15:9 light:dark cycle into their experiment, they neglected to simulate natural variations in UVR due to time of day, cloud cover, solar altitude, or shading. As a result, Bingham & Reitzel (2000) estimated that the artificial UVB exposures used in Bingham & Reyns (1999) were 500% higher than natural levels. Surprisingly, adult survival of ascidians was greater (14 d) under these conditions than under natural sunlight (2 d). The unexpected outcome was not related to the increase in UVB levels, but, instead, was most likely attributable to UVA and PAR intensities, which were 3000% below ambient. This demonstrates, very clearly, the difficulties in duplicating natural solar radiation in the laboratory setting.

Second, comparisons among different laboratory studies are troublesome (Hardy & Gucinski 1989). Differences in methodologies and experimental equipment create inconsistencies in biological dose rates (Smith & Baker 1989), spectral output, measurements of UV, and the units of value. Often, these anomalies

make data across studies incomparable. In some instances, no irradiance values are given (i.e. UVA). It is unclear if this is because the experimental apparatus did not emit those particular wavelengths, or, rather, that it was not measured or reported. Regardless, such inconsistencies are confusing to the reader and make it particularly difficult to relate to different studies.

Not all laboratory studies have used artificial UVR sources. Some were conducted outdoors, using mesocosms (Biermann et al. 1992; Fitt & Warner 1995; Nozais et al. 1999) or aquaria (Jokiel 1980; Jokiel & York 1982; Bingham & Reitzel 2000). These types of experiments have the benefits of natural radiation, as well as the ability to alter ambient UV levels, make long-term observations, and—most notably—assess the effects at the community level (Nozais et al. 1999). And, as Nozais and his colleagues point out, the high variability of environmental factors in field habitats (e.g. intertidal zone) may mask subtle UVB effects.

The Aims of this Thesis

The main objective of this thesis was to assess the ecological impacts of solar UV radiation on subtidal macrobenthic marine assemblages. To do this, I designed and deployed manipulative field-experiments in temperate Australia and Antarctica (Figure 4), which examined assemblages developing on experimental panels under different light treatments. Light regimes were created by filtering out portions of the solar spectrum with transparent UV cut-off filters. The advantages of this methodology are that assemblages are developed *in situ* using natural solar

radiation.

Here I sought to address a gap in the current scientific understanding of the ecological effects of natural UVR on macrobenthic assemblages in the shallow subtidal marine environment. Without a clear understanding of how assemblages in natural marine environments respond to ambient levels of UVR, it will be difficult, if not impossible, to accurately evaluate the ecological consequences of elevated levels of UVB caused by stratospheric ozone depletion. Thus, the general aim of this thesis was assess the responses of benthic marine assemblages to current levels of ambient UVR. This will provide valuable insight into the role of UVR in marine systems and thereby enable us to make more informed predictions about potential increases in UVB radiation in the future.

More specifically, the main questions addressed in this thesis were (1) What are the community-level effects of natural UVR on shallow-water benthic marine assemblages? That is, does UVR influence community structure, species diversity, and the biomass of assemblages?, (2) Is UVR an abiotic force that can cause structural changes in subtidal benthic marine assemblages? If so, which is more influential—UVB or UVA?, and (3) Are the impacts of UVR general? That is, are the impacts of UVR the same at global spatial scales (e.g. Antarctica and Australia)?

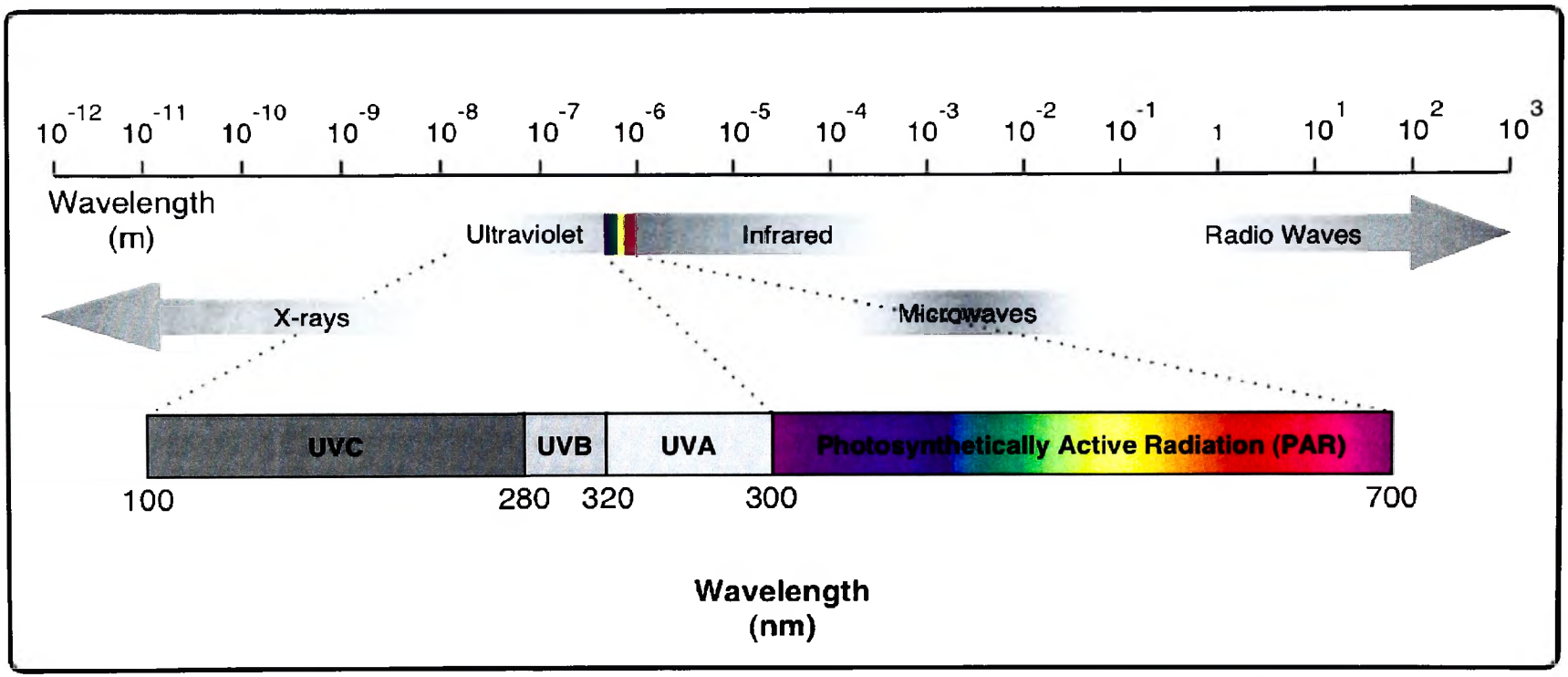


Figure 1. Diagram of the electromagnetic spectrum. The zoomed portion of the diagram shows the wavelengths (nm) for ultraviolet radiation and photosynthetically active radiation (PAR). Note: UVC portion of the ultraviolet spectrum does not reach the surface of the earth and therefore is not a critical component of this study.

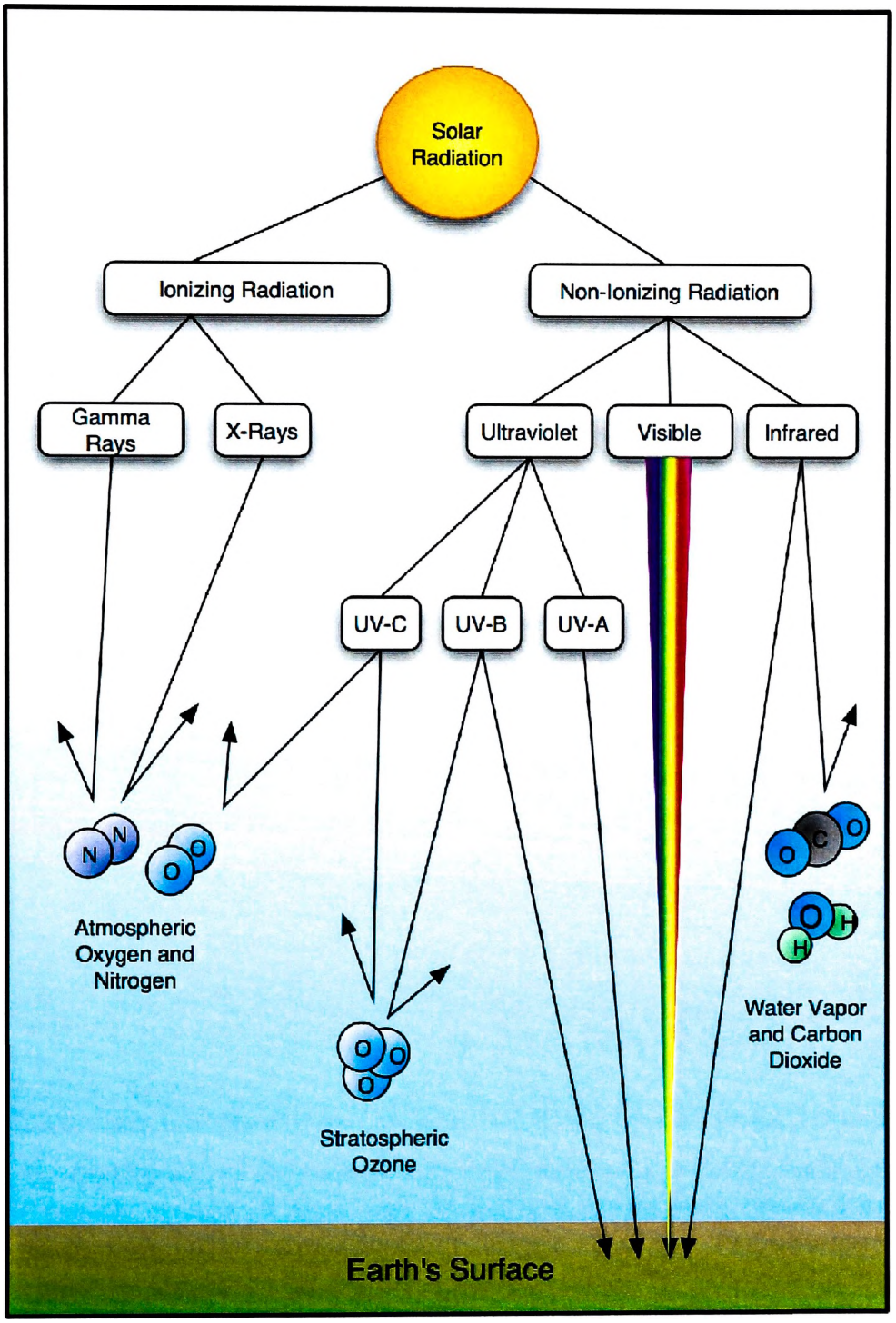


Figure 2. Interaction of solar radiation with Earth's Atmosphere. Only visible light and portions of both the ultraviolet and infrared regions reach the surface of the Earth unimpeded. Of particular interest is the fact that ozone effectively blocks out the most biologically harmful ultraviolet rays.

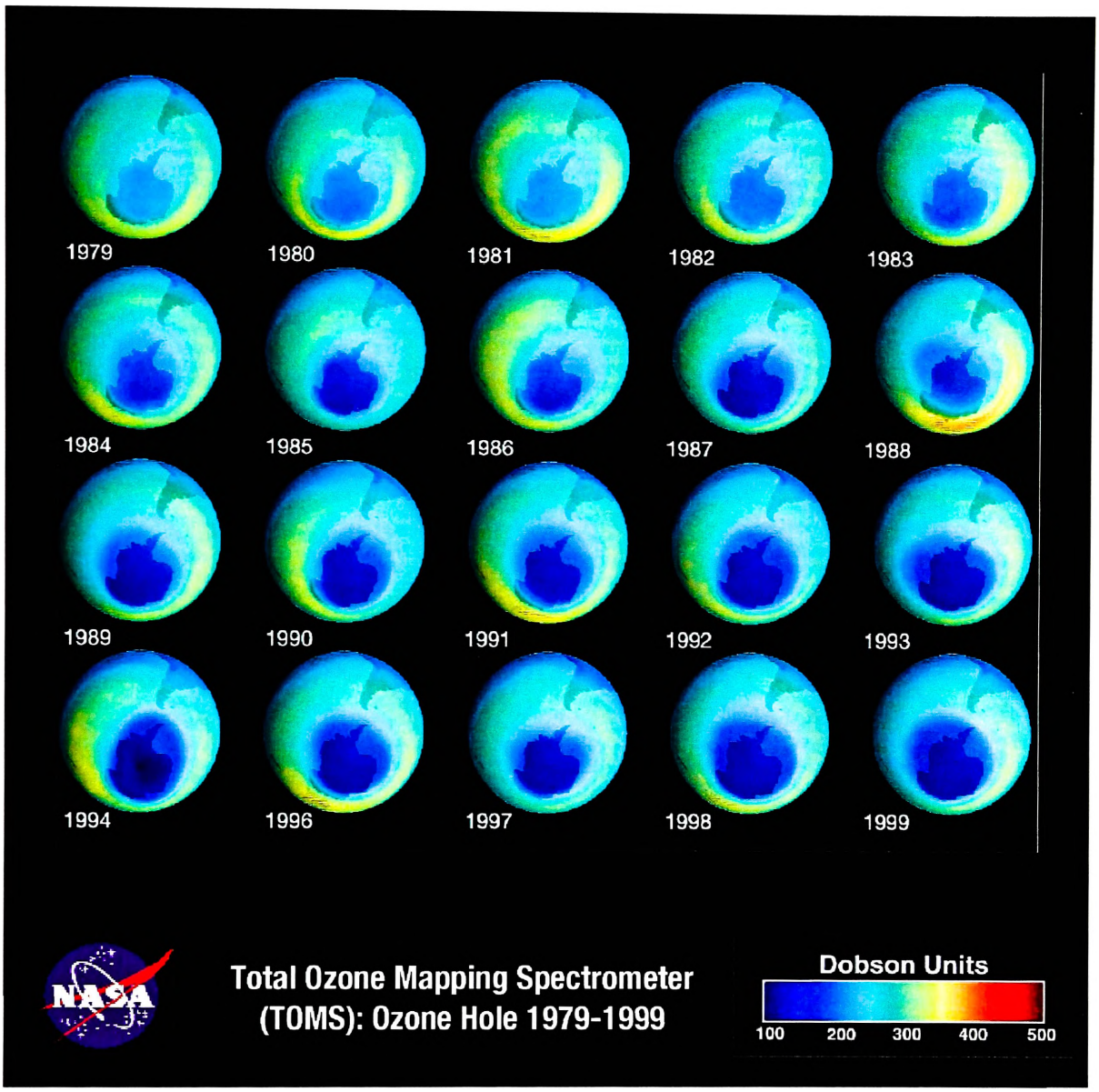


Figure 3. The development of the Antarctic ozone hole from 1979 to 1999. The mosaic shows September monthly averages of ozone over Antarctica as measured by NASA's Total Ozone Mapping Spectrometer (TOMS) aboard Nimbus 7, Meteor 3, and Earth Probe spacecraft. Dark blue areas represent regions of very low ozone concentration (<100 Dobson Units, DU) in the stratosphere. Pre-ozone hole levels would normally appear green, indicating a measurement of about 300 DU. No data were available for 1995 because no TOMS instruments were in orbit.

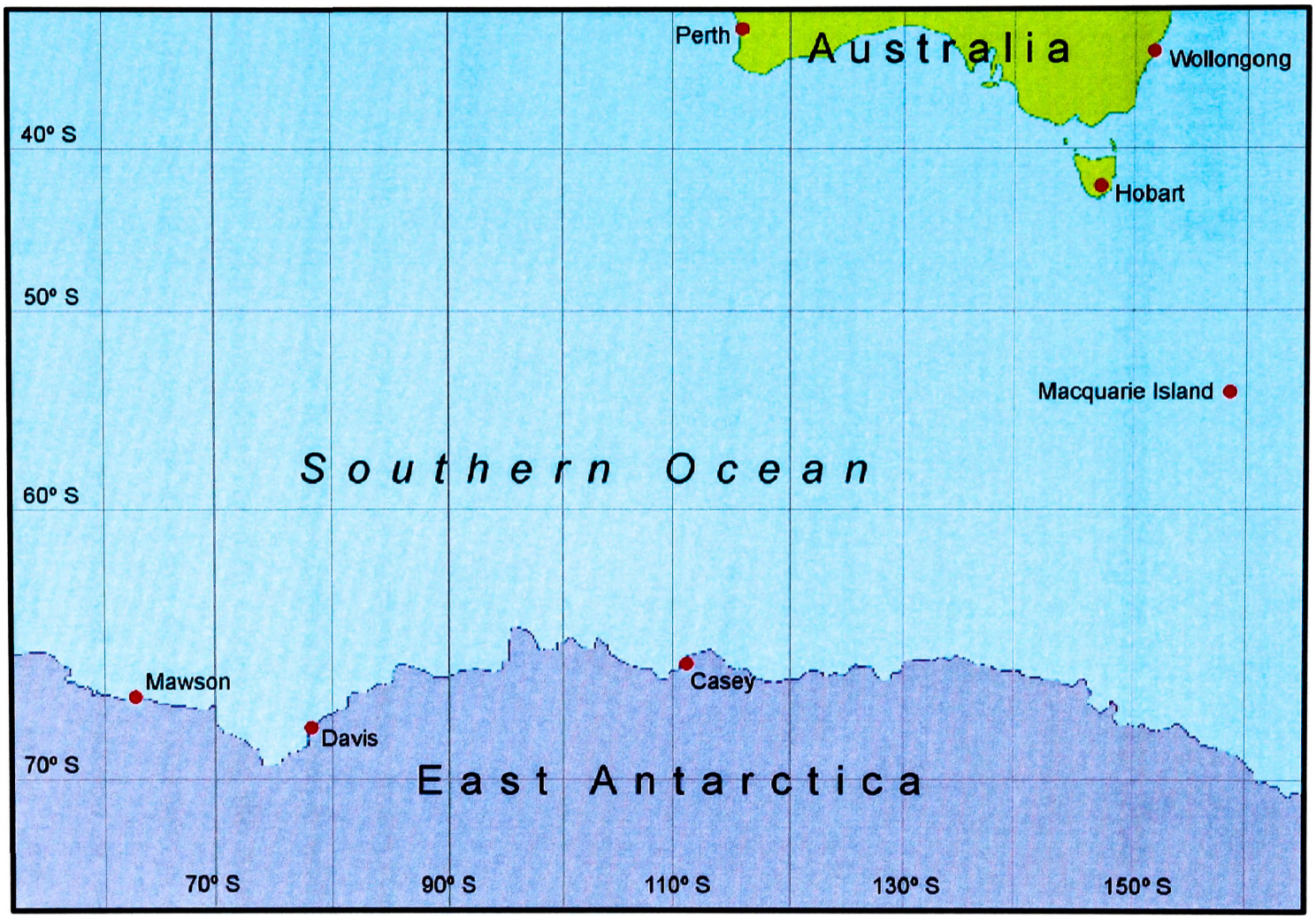


Figure 4. Map of the Southern Ocean showing the location of Casey Station, Antarctica (66.16°S 110.30°E) and Wollongong, Australia (34.45°S 150.88° E). Casey is approximately 4000 km due south of Perth, Australia.

Chapter 2
Benthic Marine Diatom Assemblages in Antarctica

A Country doomed by Nature never once
to feel the warmth of the Sun's rays, but to lie
forever buried under everlasting snow and ice.

—Captain James Cook, On Antarctica

Introduction

The most widely known consequence of human-induced stratospheric ozone depletion is the Antarctic ozone hole. The ozone hole appears annually over the Antarctic continent and surrounding Southern Ocean during the Austral spring (Sept-Nov), and has done so now for over two decades (Staehelin et al. 2001). Because ozone depletion leads to the increased transmission of biologically harmful ultraviolet-B radiation (UVB, 280-320 nm), spring UVB levels in Antarctica are equivalent to, or greater than, irradiances that occur in summer under normal ozone concentrations (Karentz 1991; Stolarski et al. 1996). It has been suggested that such increases in UVB could invoke taxonomic shifts in the

structure of marine phytoplankton communities, due to interspecific differences in UVB tolerance (Davidson et al. 1996; Karentz 1991). Although UVB is generally regarded as more harmful, UVA radiation, which is not influenced by ozone concentration, has also been shown to exhibit strong biological effects because UVA wavelengths account for a greater portion of the solar spectrum (Karentz 1994; Karentz & Bosch 2001).

In the Southern Ocean, the majority of research has focused on the effects of UVB radiation on phytoplankton (Voytek 1990; Karentz 1991; Häder et al. 1998; Karentz & Bosch 2001). Most of this knowledge comes from short-term laboratory experiments that examined species-specific effects of UVB. Several of these studies reported that UVB radiation contributes to reduced rates of primary production (e.g. Smith et al. 1992) and photosynthesis (e.g. El-Sayed et al. 1990), reduced growth and survivorship (Calkins & Thordardottir 1980), and depressed biomass and Chlorophyll *a* production (Worrest 1978). While valuable, these studies reveal little about community-level effects of UVB on phytoplankton communities in the natural environment.

Since phytoplankton is responsible for most of the ocean's primary productivity, it fulfills a vital role in the Antarctic marine ecosystem. Indeed, it forms the foundation of the food web on which nearly all life in the Southern Ocean is dependent (Priddle 1990). Aside from the colonial haptophyte, *Phaeocystis antarctica*, diatoms dominate Antarctic net phytoplankton communities (Davidson & Marchant 1994) and contribute to a large portion of the overall biomass in the

Southern Ocean. Despite the importance of natural Antarctic diatom communities, effects of elevated UVB on them remain unclear. Davidson and others (1994) found that mortality of diatoms did not change significantly until UVB exposure was increased to an order of magnitude higher than existing surface irradiances, however, more recently Davidson and others (1996) found that natural levels of UVB changed species composition of phytoplankton in mixed culture.

Most of the research on diatoms in Antarctica has concentrated on pelagic and epontic (sea ice) communities, while less is known about the effects of UVR on benthic communities, even though these habitats could be more vulnerable to changes in UVB. In temperate freshwater systems, it has been shown that diatom assemblages growing on hard substrata are sensitive to natural and elevated levels of UVA and UVB (Bothwell et al. 1994; Vinebrook & Leavitt 1996,1999). Unlike pelagic species, which can migrate to deeper water, or epontic species, which are protected by UV opaque sea ice, benthic species are unable, passively or actively, to avoid UVR. Vinebrooke & Leavitt (1999), suggested that, in cases such as these, where physical avoidance is not possible, photoprotective mechanisms may be an important adaptation to UV protection.

The aim of this project was to test for community-level effects of natural UVR on benthic marine diatom assemblages in Antarctica with and without the presence of consumers. To do this, I deployed two manipulative field experiments in the shallow subtidal zone near Casey Station, Antarctica (Chapter 1, Figure 4). The

primary questions addressed in this study are: (1) Do the effects of UVR alter community structure, biomass or diversity of diatom assemblages? (2) What are the interactive effects of ambient UV radiation and consumers on diatom assemblages?

Methods

Study Site

From 7 Jan to 22 Feb 2001, two manipulative field experiments were done to test the effects of solar ultraviolet radiation and consumers on shallow benthic marine assemblages near Casey Station, Antarctica (66.16°S 110.30°E). Casey Station is situated near the Windmill Islands (Wilkes Land, East Antarctica), a unique coastal region that is characterized by low (< 100 m), ice-free, rocky islands, and strong easterly winds (up to 160 km/h). The study site was located approximately 1 km due west of the station in a shallow (1-3 m), protected bay on the leeward shore of Shirley Island (Figure 5). This location was ideal for the experiment because shallow water prevented large icebergs entering from the northern end of the bay, while the island protected the experiment from easterly blizzards.

Experimental Rafts

On 7 Jan 2001, five experimental rafts were deployed on the western shore of Shirley Island. Rafts were separated by at least 50 m (to minimize the risk of losing every raft) and anchored to the bottom of the bay with up to 100 kg of weight to prevent them from being moved by waves or large pieces of drifting ice. Each raft (155 x 75 cm) consisted of eight experimental units (two units wide by four units long) joined together with 6 mm stainless steel cable (Figure 6 & 7).

Each unit was constructed from a plastic food storage container, a sheet of black, plastic coreflute, and two pieces of closed-cell polyethylene foam, for buoyancy.

Plastic containers were prepared in one of three ways—caged, uncaged, or partially caged—by cutting out the sides or drilling holes to influence consumer access (see below). Settlement panels (95 mm^2 unglazed ceramic tiles) were positioned horizontally into the bottom of each container so that when the unit was in seawater the tiles were submerged 4-6 cm underwater (Figure 7). To modify the wavelengths of solar radiation that a tile received, sheets of transparent plastic (250 mm^2) with varying spectral properties (Figure 8, Table 1) were placed on top of all but one (treatment control) of the units on each raft. Stainless steel hardware and plastic cable ties were used to hold the components together.

Two separate (but overlapping) experiments were done simultaneously on the five experimental rafts. The first experiment tested for the effects of UVR in the presence of consumers. It was a single-factor, fixed design with four levels of irradiation (No UVR, No UVB, No Filter and Acrylic). Because this experiment was examining the effects of UVR in the presence of consumers, this experiment only incorporated the four uncaged experimental units on each of the five rafts (4 levels of irradiation x 5 rafts = 20 experimental units). The second experiment only tested two of the irradiation treatments (no UVR and acrylic) in three consumer access treatments (caged, uncaged, cage control) on each of the five rafts. It was a two-factor design (both fixed) with four levels of irradiation and three levels of consumer access (2 levels of irradiation x 3 levels of consumer access x 5 rafts = 30 experimental units). Because this experiment utilized all

three consumer access treatments (Caged, Uncaged, Cage Control), there was overlap between the uncaged treatments in the first and second experiments.

It is important to mention here that due to logistical and financial constraints, it was not possible to do one comprehensive experiment that tested all four irradiation experiments with all three consumer access treatments. This would have resulted in large, costly, and unmanageable rafts with 12 experimental units (4 irradiation × 3 consumer access = 12). Also, due to damage from storms, the majority of replicates from raft five were lost. As a result, all statistical analyses were done with only four replicates instead of five (see Methods, Statistical Analyses).

Experiment One

The effects of natural solar radiation on subtidal diatom assemblages were tested, in the presence of potential consumers, by four irradiation treatments (Figure 9a). One of each irradiation treatment was randomly assigned to the four uncaged experimental units (units with sides removed) on each of the five rafts. The irradiation treatments and the filter materials used in this experiment were as follows:

(1) **No UVR:** These units were covered with a 4 mm thick sheet of Makrolon® (Longlife Plus 293; Rohm, Germany) to screen out both UVA and UVB wavelengths (280-400 nm). While Makrolon® is opaque to UV wavelengths, it

maintains consistently high transmittance (>90 %) throughout the PAR (400-700nm) region of the spectrum (Figure 8).

(2) **No UVB:** Units were covered with a 0.1 mm thick sheet of clear laser copier film (LTF NashuaCopy) placed between two layers of 3 mm thick UVR-transparent Perspex® (GS 2648; Rohm, Germany). This clear polyester film blocks the transmission of UVB wavelengths (280-320 nm), but is mostly transparent to UVA (320-400 nm) and PAR (400-700 nm) wavelengths. The Perspex® sheet was included for structural support and protection of the film, rather than to alter the spectral properties of the treatment. However, because multiple layers were used to make this treatment, transmittance of wavelengths in the UVA and PAR regions were slightly lower than in both the no UVR and acrylic treatments (Figure 8).

(3) **No filter:** This treatment was used as the treatment control and therefore was left uncovered to allow tiles to be exposed to full-spectrum (PAR + UVA + UVB) sunlight.

(4) **Acrylic:** For this treatment, two sheets of 3 mm Perspex® were placed over the unit. Perspex® is virtually transparent to both the visible and ultraviolet portions of the spectrum (Figure 8), thus making it an ideal material for a full-spectrum, procedural control.

Experiment Two

A two-way factorial experiment was used to test the effects of irradiation and consumers on assemblages of benthic diatoms (Figure 9b). In this experiment

there were two levels of irradiation (no UVR and acrylic) and three levels of consumer access (caged, cage control, and uncaged). To create the consumer access treatments, plastic containers were prepared in one of three ways by cutting out the sides or drilling holes to alter consumer access. The caged treatment had 4 mm holes drilled into all four sides of the plastic container, and the uncaged treatment had all four sides of the plastic container removed. To control for the possibility of reduced water flow through the caged treatments, a cage control was used. This treatment was identical to the caged treatment except that one of the four sides was completely removed. Thus, consumers were admitted but water flow was more similar to the uncaged treatment.

Data Collection

On 22 Feb 2001, 36 tiles were removed from the experimental units and placed in individually-marked zip-lock bags partially filled with seawater (~200-600 ml). The samples were returned to the laboratory, where they were stored in a dark refrigerator. Only 36 tiles were retrieved, because one of the five rafts was damaged and four of the experimental units were lost.

To process each settlement panel, all the material was scraped from a tile and placed in a beaker with the remaining contents of the bag (seawater and dislodged components of the assemblage). Filtered seawater was then added to the contents of the beaker to create a 1 L solution. The beaker was then placed on a magnetic stirring plate to keep the mixture homogenous, while 10 mL samples were collected from the solution with a pipette. Two sets (n = 35) of 10

mL samples were collected; one set for microscopy and another for spectrophotometry. The 10 mL samples collected for microscopy were individually stored in small vials in a 1% solution of gluteraldehyde and kept in a dark refrigerator at 15°C, until they could be analyzed on return to Australia. Only 35 of 36 tiles were sampled due to an error in the laboratory. An additional set of samples was collected for spectrophotometric analysis.

Spectrophotometric analysis was used to measure the concentration of photosynthetic pigments contained in a sample and thereby estimate the biomass of diatoms on tiles. Pigment extractions and spectrophotometric analysis were done as described by Clesceri and others (1998), except that in this case 90% methanol rather than acetone as a solvent was used, and the acidification times (to correct for the presence of pheophytin *a*) were 60 s rather than 90 s. Methanol is an acceptable substitute for chlorophyl extraction and is often used not only for convenience but also for safety during transport (Bleakley, personal communication).

Diatom Extraction and Analysis

Samples separated for diatom analysis were added to 40 ml of distilled water in 50 ml beakers and thoroughly mixed. Material was settled for 8 hrs and the supernatant was then siphoned off. Next, 15 ml of 15% H_2O_2 was added to the sample. Samples were then watched carefully for any excessive reaction to ensure that no material was lost as a result of an uncontrolled reaction. Beakers containing samples were left for about 2 hours and then placed in a water bath at

50°C for a further 3 hours. Samples were removed from the water bath and about 15 ml of 10% HCl was added and again watched carefully for any excessive reaction. If the reaction was not excessive, samples were placed in the water bath for a further 4 hours. The beakers were then topped up with distilled water and the samples were left to settle overnight. The supernatant was then siphoned off, again. The samples were then washed and settled a further 2 to 3 times. Cover slips were placed in evaporation dishes and aliquots of diatom residue were added to the trays with distilled water containing a tiny amount of dissolved glycerol. The samples were left to evaporate onto the slips and the base of the evaporation trays, and slips were mounted onto slides using Naphrax. Three slides were made for each sample. Diatoms were identified and counted at 1000 x magnification using phase contrast on a Leica DME microscope. Diatoms were counted along 2 separate horizontal transects from randomly-selected locations on each of the 3 slides made for each sample until at least 600 diatoms were counted for each sample.

Statistical Analyses

Univariate analyses were done using single-factor and multi-factorial ANOVAs with JMP v4.0 statistical software. Because a fifth replicate was missing from more than one treatment, data were removed to maintain a balanced design (n = 4 in all tests). Although identical sample sizes are not required for single-factor ANOVAs (Zar 1999), the design was kept balanced to keep the precision of estimates of variances similar (Underwood 1997). In one case, multiple replicates

were missing from one treatment (n = 3). Here, a 'dummy replicate' was created with the mean of the original three replicates (as described in Underwood 1997). Variances were homogenous (Cochran's test, $P > 0.05$) for all but one of the analyses. In this case, data were arc-sin transformed, but this failed to remove the heteroscedasticity of the variances. However, I proceeded with the analysis anyway because of the robustness of ANOVA with balanced data sets (Underwood 1997). Nonetheless, in these situations it is important to interpret the data with caution.

Single-factor and two-factor multivariate analyses of assemblage composition were done with PRIMER v4.0 (Clarke 1993) and NP-MANOVA (Anderson 2001) computer programs. A matrix of similarities between each pair of samples was calculated using the Bray-Curtis similarity coefficient. Data were fourth-root transformed to reduce the effect of the most abundant species (Clarke & Warwick 1994). Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional plots to illustrate patterns of difference between treatments. Stress values were less than 0.20, indicating that plots were valid representation of the patterns.

In both multivariate analyses, the null hypotheses of no differences among treatments were tested with NP-MANOVA instead of ANOSIM because the latter is unable to detect multivariate interactions in two-factor analyses (Underwood 1997a). Analyses were conducted on balanced data sets, as is required by NP-MANOVA. For all multivariate tests of hypotheses, 999 permutations were used

(Manley 1997) and permutations were done on the raw data because this method does not need large sample sizes (Gonzales & Manley 1998).

Exploratory analyses to identify which species contributed the most to differences among treatments was done using the PRIMER program SIMPER (similarity percentages). This type of analysis is not a means for statistical testing; it simply identifies which species are principally responsible for differences between samples so that further testing (on the appropriate species) can proceed (Clarke & Warwick 1994). As a result of the multivariate exploratory analysis, two additional univariate analyses were done on the three most abundant diatom species.

A priori tests on the power of these analyses were not possible due to the lack of preliminary data. Furthermore, because of the extreme costs and logistical constraints associated with conducting research in the Antarctic environment, a pilot study to obtain this data was not feasible. As such, it is noted that small sample sizes and high variability among samples in this study may result in the low probability of detecting significant irradiation effects.

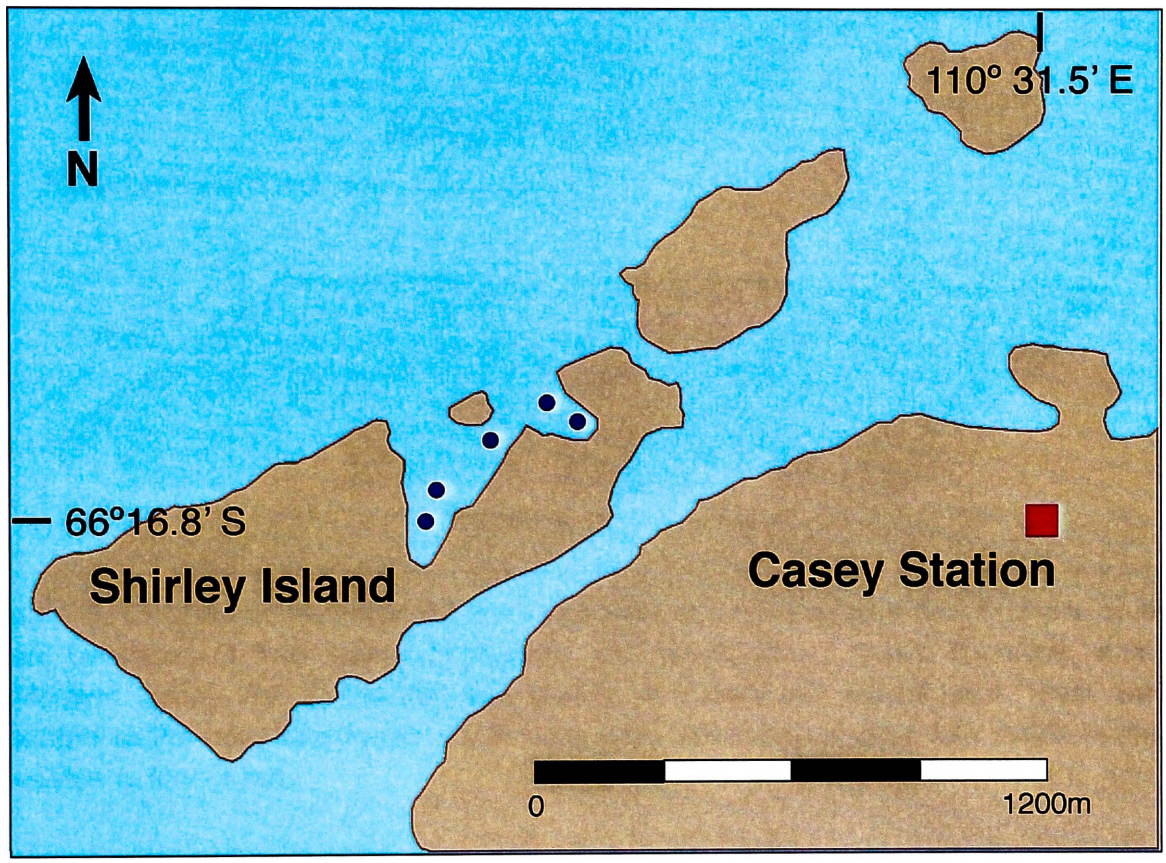


Figure 5. Map of Shirley Island study site near Casey Station, Atarctica. Blue dots represent approximate location of experimental rafts.

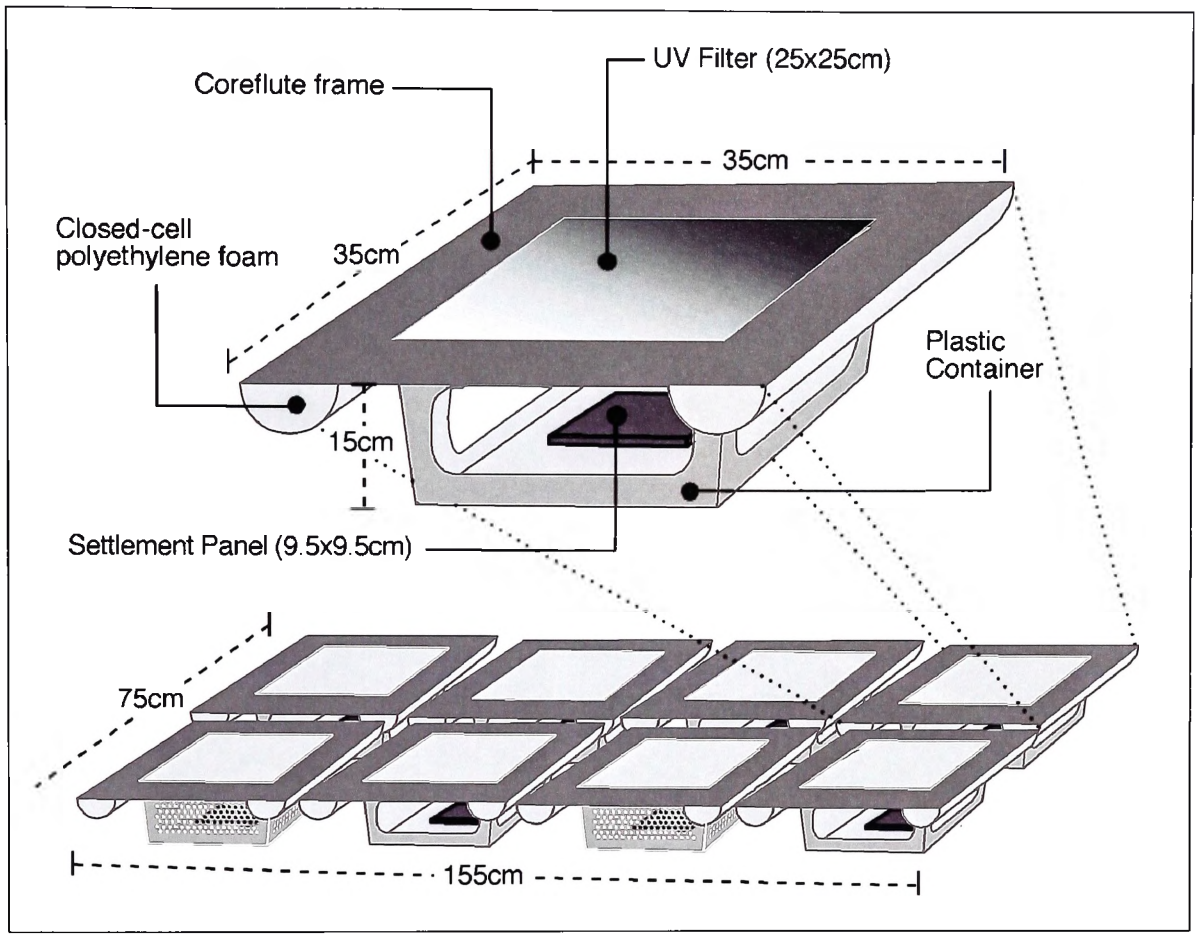


Figure 6. Diagram of experimental units and rafts that were used in the Antarctic study. Units consisted of four main components: UV cut-off filters, plastic container, and a settlement panel. For buoyancy, two pieces of closed-cell polyethylene foam were mounted to the core-flute frame. Eight units were fastened together with stainless-steel hardware to form a raft.

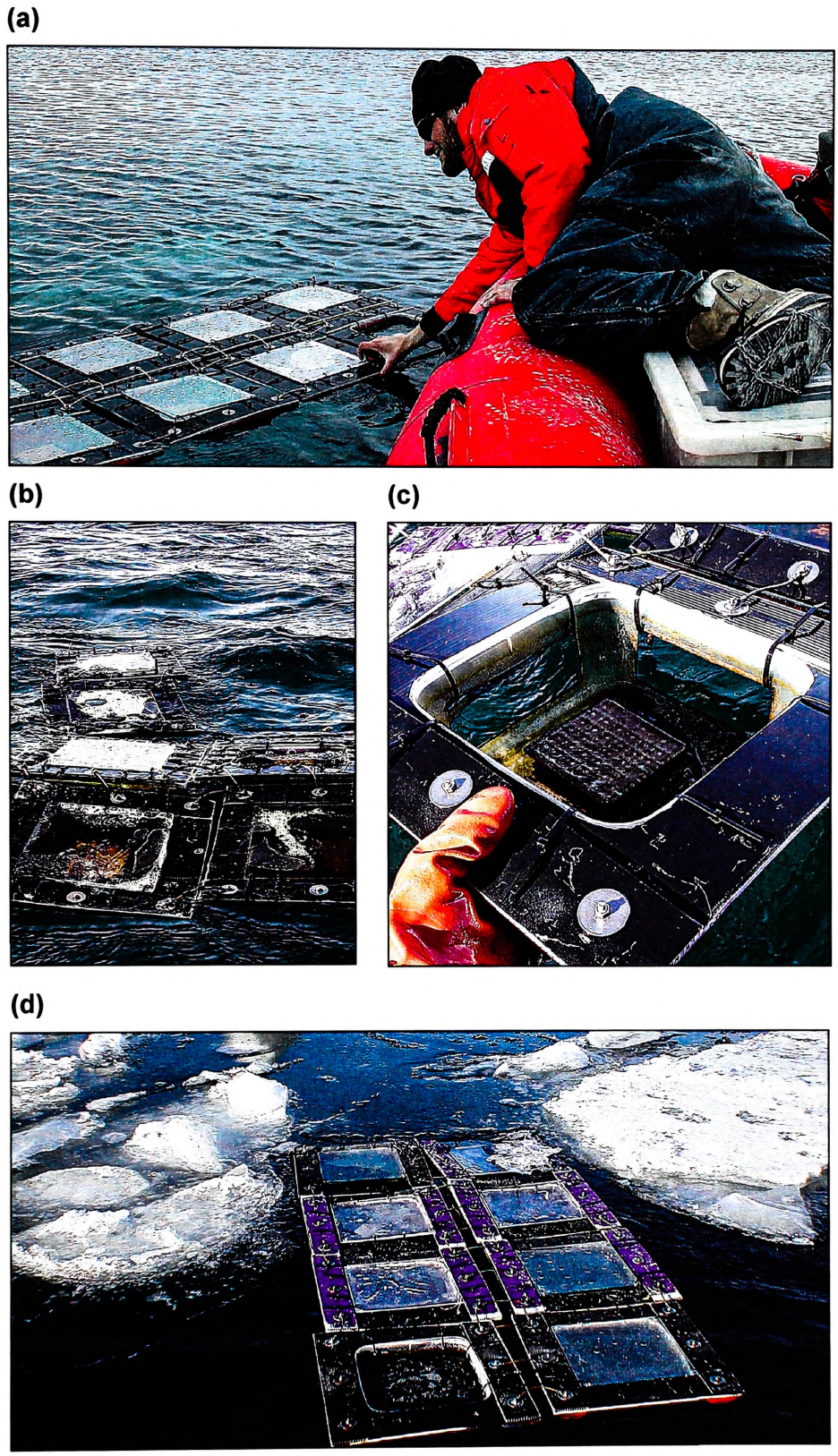


Figure 7. Photos of experimental rafts in the field near Casey Station, Antactica: (a) Author getting ready to clean the filters, (b) Raft damaged by ice, (c) Close up of the no filter treatment with settlement panel, and (d) Raft in between pieces of sea ice.

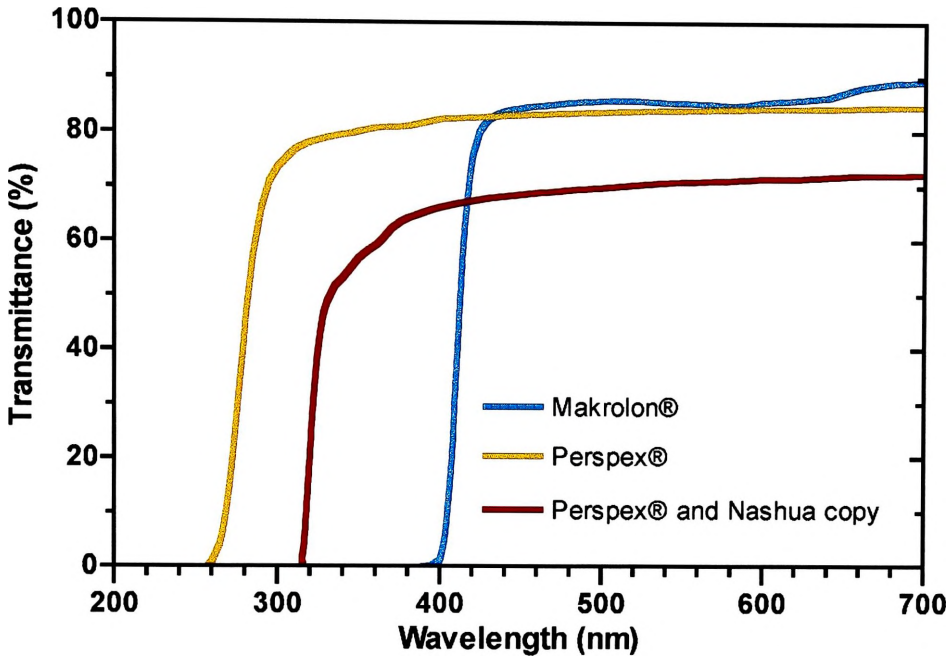


Figure 8. Spectral transmission properties of the filter materials used in the experiments near Casey Station, Antarctica. Transmittance data were collected using a Shimadzu UV-Visible spectrophotometer (Model #UV-1601; Shimadzu, Australia).

Table 1. The irradiation treatments used in the Antarctic study and a summary of the characteristics of the filter materials.

Name	Function	Radiation transmitted	Wavelengths transmitted	Filter materials	Manufacturing information
No UVR	UVR block	PAR only	400-700 nm	Makrolon®	LongLife Plus 293; Rohm, Germany
No UVB	UVB block	PAR + UVA	320-700 nm	Nashua Copy & Perspex®*	LTF NashuaCopy
Acrylic	Procedural Control	PAR + UVA + UVB	280-700 nm	Perspex®	GS 2648; Rohm, Germany
No Filter	Treatment Control	PAR + UVA + UVB	280-700 nm	-	-

*film was placed between two layers of Perspex® for structural support
PAR = Photosynthetically Active Radiation

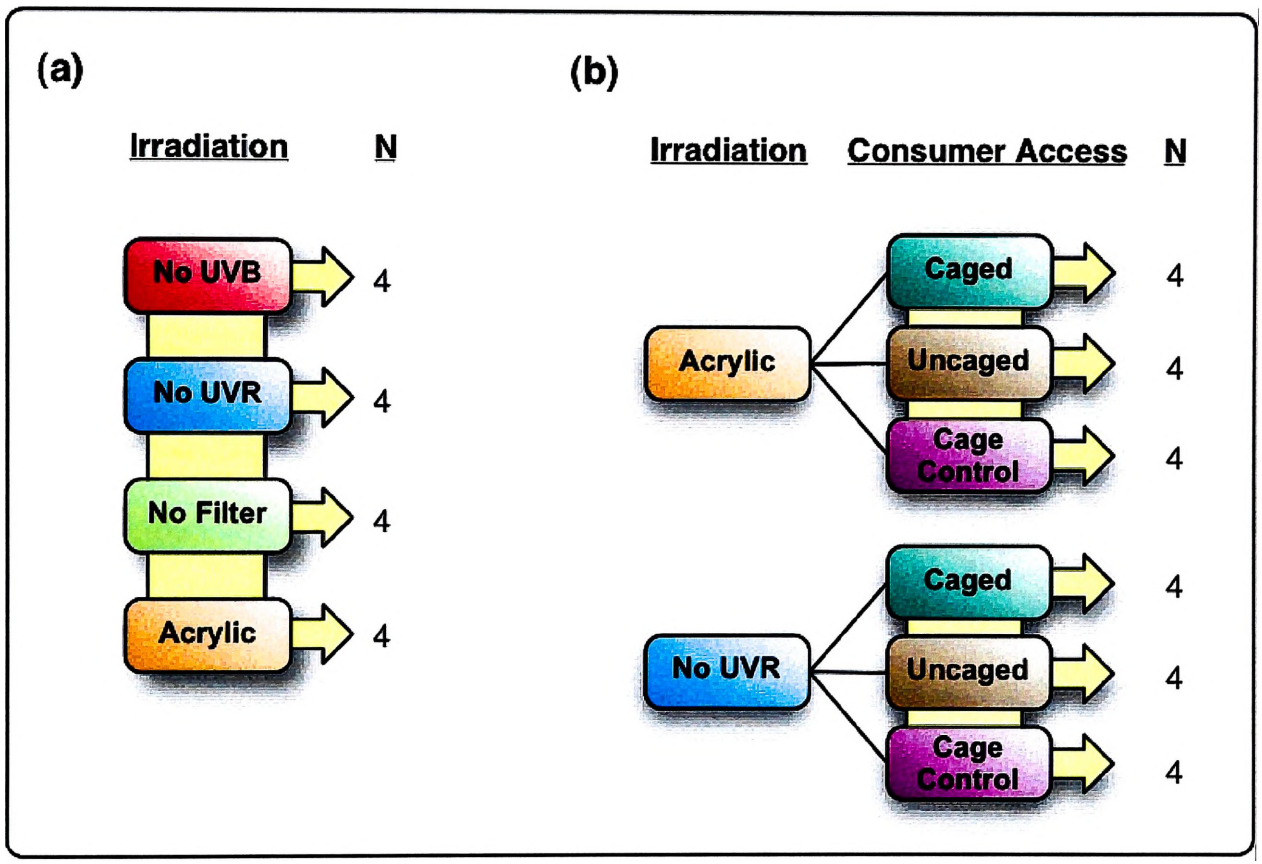


Figure 9. Experimental design layout for experiment one (a) and experiment two (b) in the Antarctic study. Experiment one uses a single-factor, fixed design with four levels of irradiation. Experiment two is a two-factor design with four levels of irradiation (fixed) and three levels of consumer access (fixed).

Results

After 46 d in the field, assemblages on settlement panels were completely dominated by diatoms. Overall, 77 species of diatoms were recorded on the 35 experimental panels. Three of those species, *Fragilaria striatula, Acanthes brevips, and Navicula glaciei,* accounted for 77% of the total diatom abundance. A silicoflagellate, *Distephanus speculum,* was also present on some of the tiles, but its abundance was extremely low (< 0.5 %).

Experiment One

There were, on average, more species of diatoms in the acrylic and no UVR treatments than on the other two treatments (Figure 10a). Likewise, diatom biomass was greatest under these treatments as well (Figure 10b). Nonetheless, single-factor ANOVAs revealed that differences in species richness and diatom biomass were not significant (Table 2).

Non-parametric multivariate analysis of variance (NP-MANOVA) on assemblage composition revealed significant differences among panels under the different irradiation treatments (Table 3). The nMDS ordinations, illustrating differences among treatments, showed that assemblages under the no-filter treatment were distinctly different from all other treatments (Figure 11). Furthermore, pairwise tests confirmed that the assemblages under the no-filter treatment differed significantly from the other three irradiation treatments (Table 3).

Exploratory analysis of assemblage composition with SIMPER revealed that the

three most abundant species—*F. striatula, A. brevips, and N. glaciei*—contributed most to differences among irradiation treatments. Further examination of this showed that relative abundance of these three species was consistent among all treatments (Figure 12). Two-factor univariate analysis revealed no significant effect of irradiation on relative diatom abundance, and confirmed that the relative abundance of the three diatom species was unaffected by UVR (Table 4).

Experiment Two

In all consumer access treatments, diatom species richness was, on average, higher under the acrylic treatment than the no-UVR treatment (Figure 13a). The same pattern was observed for diatom biomass, except for in the caged treatment where biomass was higher under the no-UVR treatment (Figure 13b). As in experiment one, univariate analyses showed that there were no significant differences in species richness and biomass (Table 5).

Multivariate analyses, however, revealed significant effects of irradiation and consumer-access (Table 6). A two-factor nMDS ordination showed that assemblages under full-spectrum radiation (acrylic) were different in all consumer access treatments, while treatments excluding UVR were only different in the caged and uncaged treatments (Figure 14). In addition, there was a distinct irradiation effect, but only in the caged consumer access treatment (Figure 14). Pair-wise *a posteriori* tests with NP-MANOVA confirmed these patterns, showing that differences among assemblages were significant (Table 6).

Once again, exploratory analysis of assemblage composition with SIMPER

showed that *F. striatula, A. brevips, and N. glaciei* were the species that contributed most to differences among assemblages in multivariate analyses. The relative abundance of these three species was fairly consistent among most treatments except for the caged, acrylic treatment, where the abundance of *F. striatula* declined and the relative abundances of *A. brevips* and *N. Glaciei* increased considerably (Figure 15 a & b). However, further examination of this data with two-factor ANOVA revealed no significant differences among irradiation or consumer access treatments (Table 7).

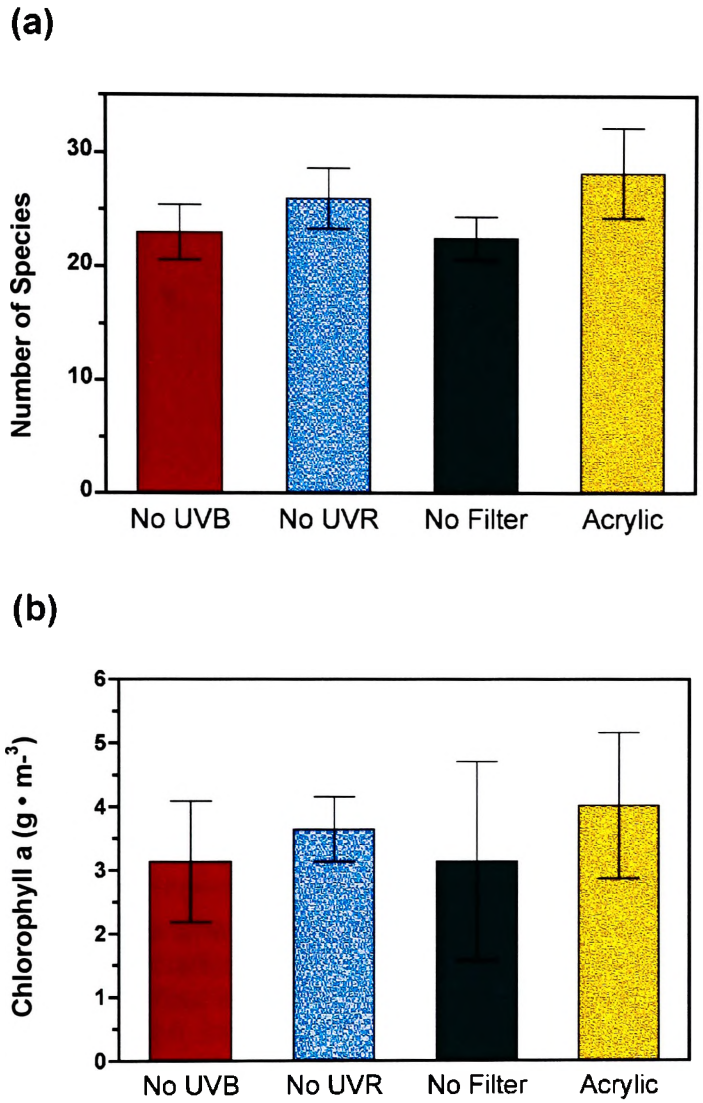


Figure 10. The effects of irradiation on mean (±SE) number of diatom species (a) and estimated mean biomass (chl a) of diatoms (b). Error bars represent standard errors.

Table 2. Analyses of the number of diatom species richness and estimated biomass (Chl a) on experimental panels (n=4) in each of four irradiation treatments with single-factor ANOVAs. Since there were missing replicates from more than one treatment, some data were removed to maintain a balanced design (see results). Data were untransformed and variances were homogeneous for each analysis (Cochran's test, $P > 0.05$).

Source	*df*	Number of Diatom Species			Estimated Biomass (Chl a)		
		MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	29.06	0.9041	0.467	0.734	0.1475	0.928
Error	12	32.15			4.925		
Total	15						

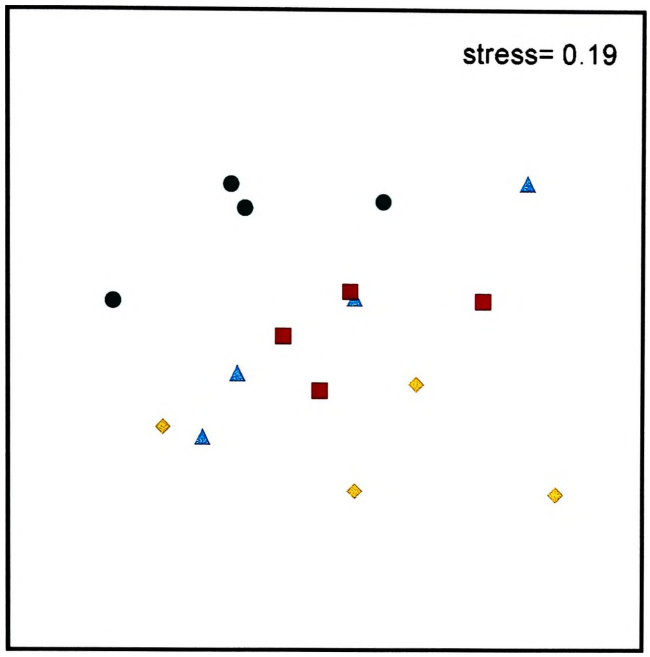


Figure 11. One-factor nMDS plot comparing diatom assemblages on experimental panels in each of four irradiation treatments: no UVB (■), no UVB (▲), no filter (●), acrylic (◆).

Table 3. Non-parametric MANOVA on Bray-Curtis distances for assemblages of marine diatoms colonizing experimental settlement panels in each of four irradiation treatments after being submersed 46 days in a sheltered bay near Casey Station, Antarctica. Data were fourth root transformed to downweight the effect of the more common species. There were 999 permutations used on all tests. Permutations were calculated on raw data due to small sample sizes.

Source	d.f.	SS	MS	*F*	*P*
Irradiation	3	2760.57	920.19	1.927	0.001
Residual	12	5731.06	477.59		
Total	15	8491.63			
Comparison*				*t*	*P*
No UVB versus No UVR				1.099	0.2390
No UVB versus No filter				1.512	0.0220
No UVB versus Full-spectrum				0.903	0.7350
No UVR versus No filter				1.751	0.0300
No UVR versus Full-spectrum				1.185	0.1670
No filter versus Full-spectrum				1.875	0.0330

*Pair-wise *a posteriori* tests among irradiation treatments

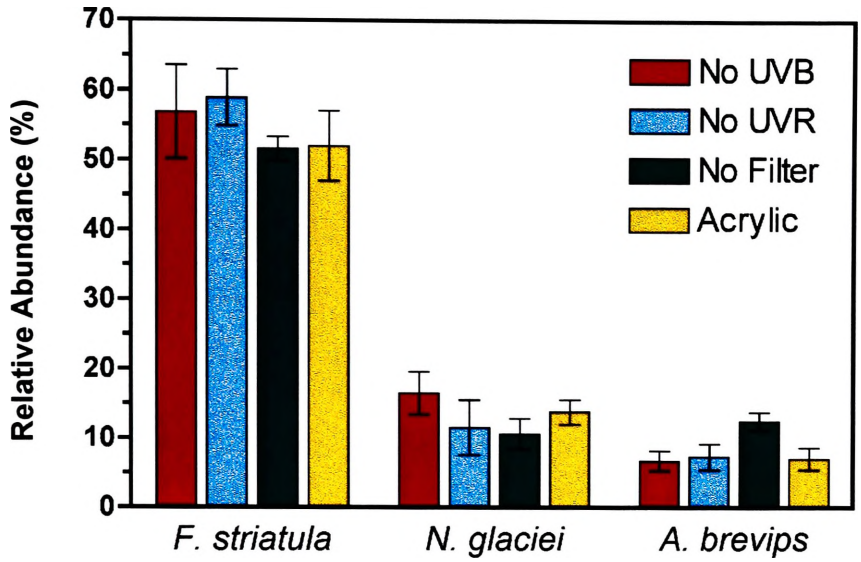


Figure 12. Mean (±SE) relative abundance of *F. striatula*, *A. brevips*, *N. glaciei*, in each of four irradiation treatments.

Table 4. Analyses of the relative abundance of *F. striatula*, *A. brevips, and N. glaciei,* on experimental panels (n=4) in each of four irradiation treatments with single-factor ANOVAs. Since replicates were missing from more than one treatment, some data were removed to maintain a balanced design (see Results). Data were untransformed and variances were homogeneous for these analyses (Cochran's test, P > 0.05).

Source	*df*	*F. striatula*			*A. brevips*			*N. glaciei*		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	52.17	0.58	0.638	27.51	0.81	0.509	29.74	2.98	0.073
Residual	12	89.82			33.68			9.96		
Total	15									

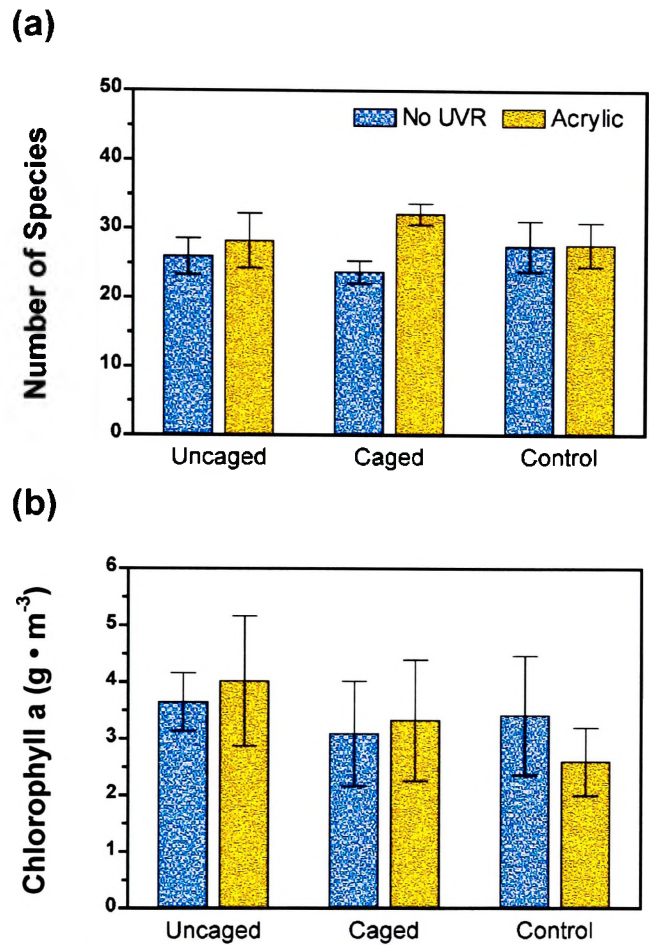


Figure 13. Mean (±SE) number of diatom species (a) and estimated diatom biomass (b) from experimental panels in two irradiation treatments (no UVR, acrylic) in each of three consumer access treatments (caged, uncaged, cage control). Error bars represent standard errors.

Table 5. Analyses of the number of diatom species and biomass (chl a) on experimental panels in each of two irradiation treatments and three consumer access treatments with two-factor ANOVAs. Both factors were fixed and orthogonal. Data were untransformed and variances were homogeneous (Cochran's test, P > 0.05).

Source	*df*	Number of Species			Estimated Biomass (chl a)		
		MS	*F*	*P*	*MS*	*F*	*P*
Irradiation	1	79.45	2.31	0.145	0.029	0.008	0.926
Consumer Access	2	1.40	0.04	0.959	1.497	0.444	0.648
Irradiation × Consumer Access	2	36.24	1.05	0.368	0.836	0.248	0.782
Error	18	34.30			3.370		
Total	23						

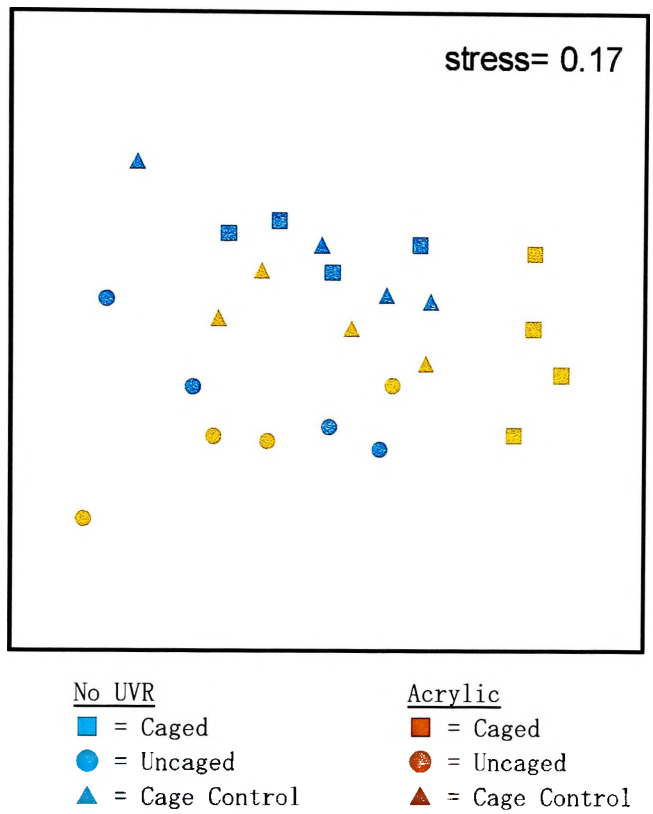


Figure 14. Two-factor nMDS plot of diatom assemblages developed on experimental panels under two irradiation treatments (No UVR, Acrylic) in each of three consumer access treatments (caged, uncaged, cage control).

Table 6. Non-parametric MANOVA on Bray-Curtis distances for assemblages of diatoms colonizing experimental panels after 46 days in a sheltered bay near Casey Station, Antarctica. Panels were placed under acrylic or no-UVR filters and housed in three different consumer access treatments: caged, cage control, and open. Data were fourth root transformed to downplay the effect of the more common species. There were 999 permutations used on all tests and permutations were done on the raw data because of small sample sizes (n = 4).

Source	d.f.	SS	MS	F	*P*
Irradiation	1	1077.44	1077.44	2.227	0.0190
Consumer Access	2	2880.69	1440.35	2.977	0.0010
Irradiation × Consumer Access	2	1895.92	947.96	1.959	0.0090
Residual	18	8709.23	483.85		
Total	23	14563.29			

Comparison[1]	*t*	P
Caged versus cage control	1.373	0.0620
Caged versus open	1.839	0.0010
Open versus cage control	1.561	0.0010

Comparison[2]	No UVR	Full-spectrum
Caged versus cage control	1.030	1.713*
Caged versus open	1.761*	1.968*
Open versus cage control	1.390	1.419*

Comparison[3]	Caged	Cage Control	Open
No UVR versus Full-spectrum	2.099*	1.000	1.185

[1]Pair-wise *a posteriori* tests among consumer access treatments.
[2]Pair-wise *a posteriori* tests among consumer access treatments within each irradiation treatment using the t-statistic.
[3]Pair-wise *a posteriori* tests among irradiation treatments within each consumer access treatment using the t-statistic.
*$P<0.05$

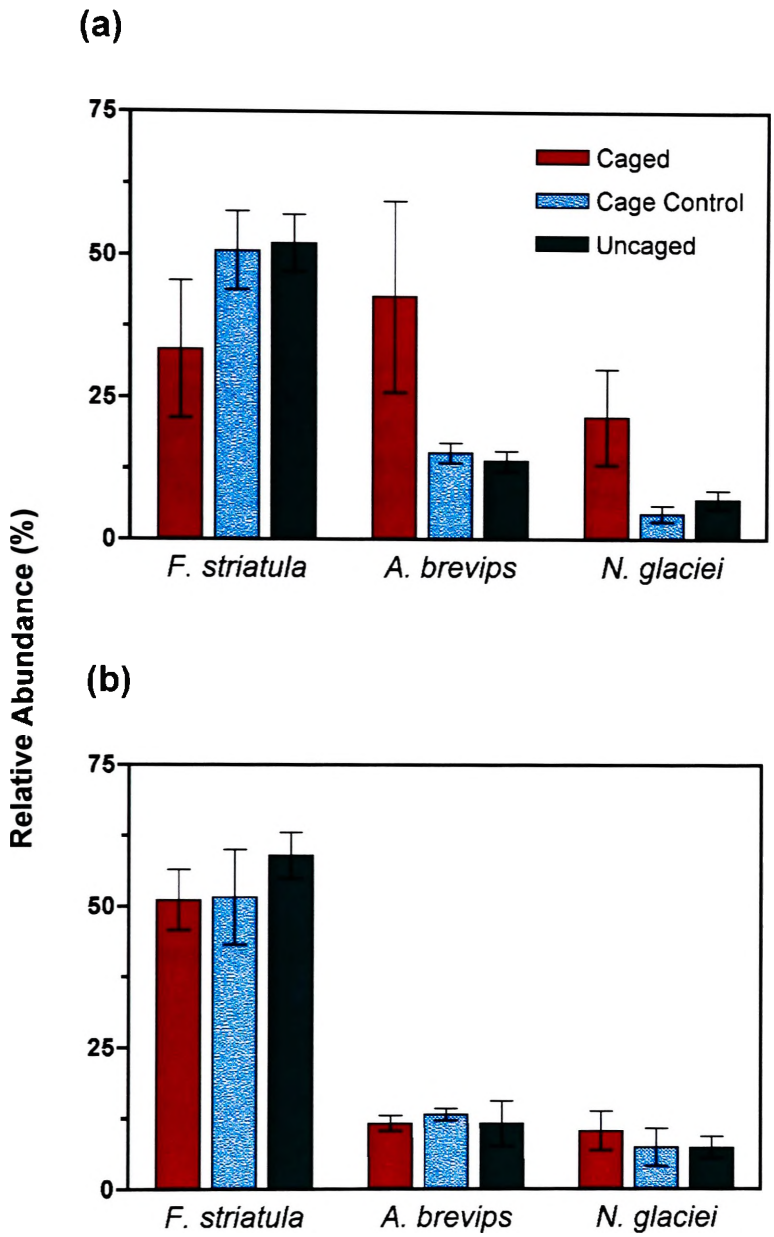


Figure 15. Mean (±SE) relative abundance of *F. striatula*, *A. brevips*, and *N. glaciei* in each of three consumer access treatments with the acrylic (a) or the no-UVR (b) irradiation treatments.

Table 7. Analysis of the relative abundance of *F. striatula, A. brevips,* and *N. glaciei* observed on experimental panels in each of two irradiation treatments and three consumer access treatments. Variances for *A. brevips,* and *N. glaciei* were not homogeneous (Cohran's test, $P < 0.05$). Though data were arcsin-transformed, this did not remove the heteroscedasticity, but the analysis was done anyway, because of the robustness of ANOVA with balanced designs.

Source	*df*	*F. striatula*			*A. brevips*			*N. glaciei*		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	1	435.8	1.95	0.179	834.1	4.07	0.058	43.8	0.642	0.433
Consumer Access	2	363.1	1.62	0.224	502.2	2.45	0.114	234.8	3.435	0.0545
Irradiation × Access	2	145.6	0.65	0.532	555.2	2.71	0.094	113.2	1.657	0.2185
Residual	18	222.8			204.8			68.3		
Total	23									

Discussion

There were no significant differences among irradiation treatments in diatom species richness or biomass. In contrast, multivariate analysis revealed significant differences in community composition in the no-filter treatment in experiment one (Figure 11) and in the caged perspex treatment in experiment two (Figure 14). However, I contend that the differences detected in the multivariate analyses were not due to irradiation effects and that UVR had no effect on the species composition of benthic marine diatoms in the manipulative field experiment. The reasoning is as follows: In the first experiment, NP-MANOVA showed that the assemblage under the no-filter treatment was different from all of the other assemblages that were covered with filters (Table 3). Because this treatment was the only one not covered, the differences here could readily be attributed to wave exposure rather than irradiance. This notion is further supported by the fact that there were no significant differences among the four irradiation treatments in the relative abundances of the three most abundant species (Table 4).

In the second experiment, multivariate analysis appeared to reveal a significant irradiation effect, but only in the caged Perspex treatment (Figure 14, Table 6). It is important to note that this treatment consisted of three replicates plus one dummy replicate created from the mean of the original 3 replicates from that treatment. For this reason, I suspect that the differences found here were anomalous, and do not pertain to any real effects of ultraviolet radiation or the

absence of consumers. This is further supported by the fact that the relative abundance of the three most common species is the same in every other treatment, in the presence or absence of consumers (Figures 12 and 15).

These findings are consistent with other studies of Antarctic diatoms. Diatoms often exhibit greater resistance to UVR exposure than other types of phytoplankton (Karentz et al. 1991; Davidson et al. 1994; Karentz 1994). For example, in a short-term laboratory study, Davidson and others (1994), showed that diatoms could withstand artificial levels of UVB two to three times higher than peak surface irradiances currently encountered in the Antarctic. Furthermore, they concluded that, with such high tolerances, changes in phytoplankton species composition as a result of UVB-induced mortality are unlikely. Similarly, Calkins and Thordardottir (1980), examined six species of Arctic diatoms and concluded that, while UV may be a significant ecological factor, most organisms would adapt to increases in UVB. McMinn and others (1994), using a different approach, examined ice cores from fjords in East Antarctica and found that there had been no significant changes in species composition of the diatom community since springtime ozone depletion began, more than two decades ago.

Contrary to our results, Davidson and others (1994), found that UVA reduced survival of phytoplankton under Mylar screens, which block UVB, but allow UVA and PAR to pass through, indicating that UVA-induced mortality is possible. It

should be noted, however, that that study was conducted in the lab with artificial radiation, and the results may therefore not apply to natural assemblages.

In other regions of the world, there is evidence that UVR can alter the structure of benthic diatom communities. In freshwater systems, research has shown that diatom assemblages growing on hard substrata are sensitive to natural and elevated levels of UVA and UVB (Bothwell et al. 1993, 1994; Vinebrooke & Leavitt 1999).

There are some indications that UVR may alter species composition in marine systems as well. In the laboratory, Worrest and others (1978), examined the long-term (> 1 mo) effects of simulated solar UV on a marine community using a flow-through seawater system, and found that higher levels of UV-B radiation reduced the species diversity of diatoms. In Greece, Santas and others (1997), showed that UVB caused shifts in species composition of diatom assemblages grown on ceramic tiles in the field, but during later stages of succession (~1 mo) the differences in community structure became less pronounced. Because these differences did not persist through later successional stages, it was concluded that in some cases, diatoms are capable of mitigating UV-induced stress (Santas et al. 1997). Since panels in my experiments remained in the field for more than six weeks before samples were collected, it is possible that any changes in species composition had already occurred and that the diatoms under full-spectrum treatments had time to adapt to the presence of UVR.

As mentioned above, Vinebrooke & Leavitt (1999) have suggested that benthic

species could be susceptible to UVB exposure, because they are incapable of physical avoidance. Consequently, it has been proposed that photoprotective mechanisms will be an important adaptation for benthic diatoms. Diatoms are known to contain UV-absorbing compounds, such as Mycosporine-like amino acids (MAAs)(Marchant et al. 1991; Helbling et al. 1996; Riegger & Robinson 1997). However, the extent to which diatoms rely on MAAs for protection is not clear. For example, Davidson and others (1994), showed that diatoms are capable of surviving UVB irradiances 3 to 5 times greater than *Phaeosystis antarctica*, yet the concentrations of UV-absorbing compounds in the diatoms were 2 to 5 orders of magnitude less than the concentrations in *Phaeocystis*.

Conclusion

The results of this study indicate that UVR has no effect on species composition, richness, or biomass of benthic marine diatoms in Eastern Antarctica. To my knowledge, this is the first manipulative field-based examination of the effects of UVR on the species composition of Antarctic diatoms. Although these results conform to other previous findings in Antarctica, other studies around the world have indicated that UVR may indeed have impacts on the species composition of benthic diatoms. The species-specific effects of UVR on diatoms in short-term laboratory experiments are well documented, and evidence indicates that diatoms vary widely in their tolerance to UV. However, to extrapolate these findings to the natural environment is difficult and should be done only with caution.

As previously mentioned in the methods section, small sample sizes and high

variability among samples in this study may yield low power in the statistical analysis. This may result in a low probability of detecting significant effects even though real differences among irradiation treatments may be present (i.e. large Type II errors). Nevertheless, these results are in accordance with previous studies of diatoms in Antarctica, and suggest that these are robust organisms, capable of adapting to natural levels of UVR. While the presence of UV-absorbing compounds like MAAs may, in part, explain their resilience, other mechanisms may be involved. In any case, to better understand the impacts of UVR on benthic diatom communities, more long-term, manipulative experiments must be conducted in the field using natural solar radiation. Until then, the ultimate effects of UVR on the Antarctic marine ecosystem remain uncertain.

CHAPTER 3:
Benthic Marine Assemblages in Temperate Australia

I love a sunburnt country,
A land of sweeping plains,
Of ragged mountain ranges,
Of droughts and flooding rains.

—Dorothea Mackellar

Introduction

While stratospheric ozone depletion is most notoriously associated with the Antarctic Ozone Hole, it is important to point out that ozone depletion at high-latitudes is not the only concern. Significant losses of stratospheric ozone have also occurred at middle and low latitudes (WMO 1999; Staehelin et al. 2001), which, as at high-latitudes, leads to the increased transmission of harmful UVB radiation to the surface of the earth (Kerr & McElroy 1993). Thus, it is thought that ozone loss at mid-latitudes could have detrimental impacts on marine organisms in temperate regions.

The discovery of the Antarctic Ozone Hole in the early 1980s led to a strong

regional focus of UV research in the Antarctic and surrounding Southern Ocean. Researchers were concerned that elevated UVB levels would cause broad-scale ecological collapse by disrupting the ecosystem at the base of the food web. As a consequence, the majority of research was limited to phytoplankton and its role in primary production (e.g. Worrest et al. 1978; Calkins & Thordardottir 1980; El-Sayed et al. 1990; Smith et al. 1992) and was the subject of many reviews (Smith & Baker 1989; Häder et al. 1995; Karentz & Bosch 2001). Recently, however, some of the attention is moving away from polar regions and primary production and researchers are beginning to examine the impacts of UVR on community structure and diversity of benthic marine communities at the mid-latitudes (e.g. Santas et al. 1997; Nozais et al. 1999; Wulff et al. 1999; Lotze et al. 2002; Wahl et al. 2003, submitted).

Currently, mid-latitude ozone losses in the Southern hemisphere are about 5% below values before the 1980s. Although there is evidence that the halogen (e.g. Chlorofluorocarbons, CFCs) loading of the atmosphere is leveling off or even declining (WMO 1999; Randeniya 2002), total recovery of the ozone layer is not expected to occur until the middle of the 21st century (WMO 1999). However, these predictions are primarily based (and dependent on) the continued decrease in CFCs brought about by the Montreal Protocol.

In contrast to these predictions, a recent model developed by the Commonwealth Scientific & Industrial Research Organization (CSIRO) in Australia, shows that a rise of another ozone-depleting substance—nitrous oxide (N_2O)—may lead to

increased depletion of ozone specifically at the mid-latitudes (Randeniya 2002). Worse still, it is thought that this depletion will occur during summer when UV irradiance is at a maximum. Regardless, ozone depletion at mid-latitudes is going to be a problem for at least another fifty years and it is still uncertain how marine organisms at mid-latitudes are likely to respond to current levels of ambient UVR. Without this knowledge, it will be difficult to make predictions about the ecological consequences of elevated levels of UVR in the near future.

To date, the majority of community-level UV studies at mid-latitudes have dealt mainly with short-term experiments in the scale of days or weeks. Field-based experiments studying the impacts of natural UVR on benthic communities in aquatic ecosystems are often limited to about 30 to 45 d, whereas few studies have lasted longer than 80 d (Table 8). Little is known, therefore, about the effects of UVR on communities at longer time scales. Previous studies at shorter time scales have detected significant changes in diversity or species composition during recruitment, but these effects eventually diminish during later stages of succession (e.g. Santas et al. 1997, 1998b). However, because these studies are limited to relatively short time scales (<45 d), it is not known if impacts of UV could have long lasting impacts on benthic assemblages.

Not only are UV studies restricted to small temporal scales, but they are restricted to small spatial scales as well. Out of 14 studies examining the effects of UVR on aquatic communities in both marine and freshwater environments, just over half of them used field experiments. Among these studies, not one of the experiments

was spatially replicated to test for the effects of UVR at multiple locations. Without sufficient spatial replication in field experiments, knowledge about the generality of UVR in aquatic systems is restricted.

The aim of this project was to test for community-level effects of natural UVR on benthic marine assemblages in temperate Australia. To do this, I deployed short (~19 d) and long-term (84 d) manipulative field experiments were deployed at two study sites in the shallow subtidal zone near Wollongong, Australia. To test for the effects of natural solar UVR, assemblages were developed on ceramic experimental panels under irradiation treatments created with UV cut-off filters. The primary questions addressed in this study were: (1) Do the effects of UVR alter community structure, biomass or diversity of assemblages at short time scales? (2) Are these patterns consistent through time and at other locations? (3) Can the effects of UVR alter the structure and diversity or biomass of assemblages at longer time scales?

Table 8. The duration of field and mesocosm studies examining the community-level effects of UVR in marine (M) and freshwater (F) environments. For comparison the studies from Antarctica (Chapter 2) and Australia (Chapter 3) have been included as well. Where multiple durations are given, more than one experiment was done.

Source	Aquatic Environment	Type of Study	Duration (d)
Bothwell et al. 1994	F	Mesocosm+	30
Hill et al. 1997	F	Field	18, 32, 28
Keller et al 1997a	M	Mesocosm*	71
Keller et al. 1997b	M	Mesocosm*	31
Kiffney et al. 1997	M	Field	30
Lotze et al. 2002	M	Field	144
Nozais et al. 1999	M	Mesocosm*	43
Odmark et al. 1998	M	Mesocosm*	19
Santas et al. 1997	M	Field	43
Santas et al. 1998a	M	Mesocosm‡	42
Santas et al. 1998b	M	Field	43/35
Vinebrook & Leavitt 1999	F	Field	30
Wulff et al. 1999	F	Field	134
Xenopoulos & Schindler 2003	F	Field	2
Antarctic Study (Chapter 2)	M	Field	46
Australian Study (Chapter 3)	M	Field	19/84

+River Flumes, *Outdoor Mesocosm, ‡Indoor Mesocosm

Methods

Study Sites

The experiments in this study were conducted at two sites on the southeastern coast of Australia near Wollongong, NSW (Figure 16, inset), between 31 December 2001 and 24 March 2002. The first study site was located on the northern side of Bass Point in the south-western corner of Beaky Bay (34°35.6'S 150°53.2'E). The second site was located about 9 km south of Bass Point, on the northern shore of Kiama Harbour (34°40.1'S 150°51.2'E) (Figure 16). At both study sites, experiments were established in the shallow subtidal on a granite rocky substrate mainly dominated by urchin-grazed barrens (Underwood et al. 1991). Both study sites were located in semi-sheltered areas, but due to the shallow environment, these sites were often subjected to high wave activity and tidal currents.

Proposed Experimental Design

This study was originally designed to test the effects of UVR on benthic assemblages at two locations and at two time scales using a long-term and a short-term experiment. Unfortunately, the initial design and analysis of both experiments had to be slightly modified due to storm damage and logistical problems during the course of the experiment. The initial short-term experiment (Figure 17) was broken down from a single, three-factor design into several smaller designs for analysis (Figure 18). In the long-term experiment, the Kiama

Harbour location was completely eliminated, thus reducing an original two-factor design to a single-factor design (figure 19). Although modifications were made to the overall design, the purposes of each experiment still remained the same.

Revised Experimental Design

Short-term Experiment

For the short-term experiment, the effects of UVR on assemblages developed on experimental panels were tested by four irradiation treatments: (1) no-UVR, blocks UVA and UVB; (2) no-UVB, blocks UVB only; (3) no-filter, full-spectrum uncovered (treatment control), and (4) acrylic, a full-spectrum covered (procedural control). Two UV-blocking treatments were used so that the differential effects of UVA and UVB could be detected. Both of the control treatments were necessary to prevent the confounding of the experiment by the introduction of filter artifacts (see "UV treatments" below). The experiment was conducted at two locations to test for the generality of UV patterns. There were 5 replicates for each irradiation treatment at each location, making a total of 40 experimental units, 20 at each site.

To determine if the effects of UVR were consistent over time, this experiment was repeated consecutively four times. At the end of each time (T1-T4), experimental panels were removed from the experimental units and taken to the lab for examination. Due to logistical constraints, panels were replaced in experimental units located in the same spot with the same irradiation treatment. Data from the panels collected at the different times are, therefore, not fully independent.

Consequently, the factor "time" was not included in any of the statistical analyses in order to avoid problems associated with temporal non-independence (Glasby 1999c). Nevertheless, these data were still useful for qualitative comparisons, but should be interpreted with caution. As mentioned above, data from times 2 and 3 at the Kiama Harbour site were not available because of the damage caused by storms.

Long-term Experiment

In the long-term experiment the effects of UVR on assemblages were tested with four irradiation treatments (no UVR, no UVB, no filter, and acrylic). Due to the loss of the Kiama site, this experiment was done only at the Bass point study site, so testing the generality of the effects of UVR in the long-term was not possible. In contrast to the short-term experiment, which was repeated at four different times during the study, panels in the long-term experiment were left undisturbed in the field for 84 d.

Experimental Setup

Eighty experimental units were made to support the experimental panels (95 × 95 × 8 mm unglazed ceramic tiles) and UV cut-off filters used in this study (Figure 20a). Units were constructed with pieces of PVC electrical conduit (16 mm diameter) fitted together to create a triangular-shaped frame. Assembled, each unit measured 290 mm high, 290 mm deep, and 231 mm wide. A plastic base-plate made from 5 mm thick PVC sheeting (300 × 150 mm) was mounted across the back of the units to serve as a platform for a vertically-aligned experimental

panel. The platform was tilted slightly upward (~10°) to increase the amount of direct sunlight the experimental panel received and to minimize shading.

After the units were constructed, they were taken to the study sites and bolted to the substrate (~ 1 to 2 m apart) with stainless-steel Dynabolts® (Figure 20c & d). An effort was made to ensure that every unit (within and among locations) was placed at the same depth (±10 cm) to equalize the amount of irradiation each unit received. Therefore, depending on the tide, all units were submerged in 1 to 3 m of water. To maximize the daily exposure of solar radiation, units were installed facing North. Once the units were installed, an experimental panel was then placed into each unit by fastening it to the PVC platform with plastic cable ties. Next, each unit was randomly assigned to an experiment (long or short-term) and a UV treatment (no UVR, no UVB, no filter, or acrylic). For logistical purposes, once a unit was assigned to an experiment and a UV treatment it remained that way for the duration of the study.

Finally, transparent plastic filters (240 × 240 mm) were attached to the PVC framework above the experimental panel and fastened with plastic cable ties. For the no UVR and no UVB irradiation treatments a plastic UV cut-off filter was used to block out specific portions of the solar spectrum (see below). The control treatments were either covered with a sheet of UV transparent acrylic (procedural control) or left uncovered (treatment control). Every three to five days, experimental units were maintained and the UV filters were cleaned with a non-abrasive cloth to prevent fouling (Figure 20b). Half-way through the experiment

(~43 d), the filters were replaced to ensure that irradiation regimes did not change over time due to degradation of the filter materials.

UV Treatments

This study used the same four light treatments that were used in the Antarctic experiments: no UVR, no UVB, No Filter, and acrylic. While the treatments were virtually the same in both the Antarctic and Australian experiments, the materials used to create them were different. As a result, the spectral properties of the treatments in this study were slightly different from those of the Antarctic study (Figure 21; Table 9).

The following were the materials used to create the irradiation treatments for this study:

(1) **No UVR:** A 3 mm thick sheet of Safeguard Polycarbonate (Tsutsunaka; Tokyo, Japan) was used to block UVA and UVB wavelengths. This material maintains consistently high transmittance throughout the PAR (400 to 700 nm) region of the spectrum.

(2) **No UVB:** A thin (< 0.5 mm thick), transparent film of Mylar® (Dupont Teijin Films; Wilmington, DE USA) was attached to the underside of a 3 mm sheet of Acrylite® OP-4 (Cryo Industries; Rockway, NJ USA) with tiny cable ties. The transparent polyester film blocks transmission of UVB wavelengths, but allows more than 90% transmission of UVA and PAR.

(3) **No Filter:** This was used as a covered full-spectrum control. It allowed

uninhibited transmission of natural sunlight to reach the settlement panel. Both the acrylic Control and the No Filter treatments were used in conjunction to test for artifacts caused by placing plastic sheets above the settlement panels.

(4) **Acrylic:** One sheet (3 mm thick) of Acrylite® OP-4 was used as a covered full-spectrum control. Acrylite® OP-4 is nearly 100% transparent to both the visible and ultraviolet regions of the spectrum, making it very similar to full-spectrum sunlight.

Data Collection

Panels were collected underwater using SCUBA. Collection was done in sets of 20 panels to make the process of collection more manageable and to minimize the amount of time samples had to be stored in the lab. Each panel was carefully removed from a unit and placed vertically into individual plastic containers. The containers were cylindrically-shaped so that only two edges of the panel touched the sides of the container, thus stabilizing the panel during transport and minimizing the potential damage during the collection process. Next, the lid to the container was sealed trapping the ambient seawater. Each lid was labeled with a unique number for identification. As panels were collected, the irradiation treatment that the panel was associated with was matched with the lid number and recorded on a slate so that panels could later be identified. After collection, panels were carefully transported to the laboratory in their containers and temporarily stored in a refrigerator (5° C) until they could be individually examined (1 to 2 d).

In the lab, panels were individually examined under a dissecting stereomicroscope, in a random order, within 1 or 2 d. To eliminate bias in my observations, the treatment that the panel belonged to was not identified until the whole set was examined. Only a 70 x 70 mm area in the center of each tile was examined to avoid the potential for edge effects. Percent cover of all species was estimated with a transparent sheet marked with 100 random, 1 mm dots (1 dot = 1% cover). Organisms observed on the panel, but not under a dot were recorded as 0.5%. Nine taxa from 6 major groups were identified and recorded.

Towards the end of the experiment, I noticed that on some of the panels from the short-term experiment, a canopy of algae was obscuring the presence of spirorbids. Therefore, in an effort to gain a more detailed understanding of the effects of UVR on the spirorbids, I added an additional step to my methods for the panels from time 4. Because the algae was so dense on some of the panels and the number of spirorbids potentially very high, I decided to take subsamples, rather than examine the whole panel. To do this, I counted the number of both *Pileolaria lateralis* and *Janua steuri* in three random 2 x 2 cm squares with a stereomicroscope at 20-40x magnification and determined the average number of spirorbids per 4 cm^2.

After the panels were examined under the microscope, the total biomass (dry weight) of each tile was recorded. To do this, the center 7 x 7 area of each panel was removed and placed onto an individual piece of aluminium foil. Each

sample was then placed in the oven and dried for about 24 hr. The weights of each sample were then recorded.

Statistical Analyses

Univariate analyses in the short-term experiment were used to test the effects of UVR on the following variables: biomass, number of taxa, percent cover of algae, and mean number of spirorbids per 4 cm^2. As mentioned previously, the original design of the experiment had to be altered because data at times 2 & 3 were not available. Consequently, univariate statistical analyses were done in two ways: (1) To test for the effects of irradiation on assemblages at Bass Point only, single-factor ANOVAs were used at times 1 through 4, and (2) To test for the effects of irradiation, location, and the interaction of these factors at Bass Point and Kiama Harbour, two-factor ANOVAs were used at times 1 & 4. To avoid problems associated with temporal non-independence, "time" was not included as a factor in any analysis (Glasby 1999c).

A priori tests on the power of these analyses were not possible due to the lack of preliminary data. In addition, due to the extreme costs and logistical constraints associated with conducting a subtidal research project at two locations, a pilot study to obtain this data was not feasible. As such, it is noted that small sample sizes and high variability among samples in this study may result in the low probability of detecting significant irradiation effects.

Short-term experiment

In the short-term experiment all univariate analyses were done using single-factor and two-factor mixed model ANOVAs. For single-factor analyses the factor was irradiation, which had four levels: no UVR, no UVB, no filter, and acrylic. For the two-factor analyses the factors were location (random) and irradiation (fixed). Data were normally distributed (Shapiro-Wilk, $W > 0.05$) and variances were homogeneous (Cochran's test, $P > 0.05$) in all tests. Data in all tests were balanced, but depending on the test had either four (times 2 & 3) or five replicates (times 1 & 4). Where a single replicate was missing from one treatment group, a 'dummy replicate' was added to maintain a balanced design with five replicates (as described in Underwood 1997). A dummy replicate was created by taking the average of the remaining replicates. By using a dummy replicate, the data set was kept balanced without influencing the estimated variance or the estimated average of that treatment (Underwood 1997). The degrees of freedom were adjusted accordingly to compensate for the added datum. If one replicate was missing from more than one treatment group, a single replicate was randomly removed from each of the other treatments to even-up the data. In this case, the number of replicates for each treatment was four.

To test for differences in community structure in the short-term experiment, percentage cover estimates of taxa on panels were analyzed with single-factor and two-factor multivariate analyses. One-factor analyses were used to test for differences among irradiation treatments at times 1 to 4 at Bass Point and at times

1 and 4 at Kiama Harbour. In addition, two-factor analyses were done to test for the effects of irradiation, location, and the interaction of these factors at times 1 & 4.

Multivariate data were fourth-root transformed to reduce the effect of the more common taxa (Clarke & Warwick 1994). Non-metric multidimensional scaling nMDS was used on Bray-Curtis distances to illustrate (in 2-dimensions) patterns of difference between treatments. The stress values for each nMDS plot were less than 0.20, and therefore were interpretable 2-dimensional representations of the multivariate data (Kruskal & Wish 1978; Clarke 1993). To test the null-hypothesis of no differences in assemblage composition among treatments, two-factor NP-MANOVA was used (see Anderson 2001). In this case, NP-MANOVA was used rather than Analysis of Similarities (ANOSIM) because the latter cannot detect multivariate interactions in two-factor analyses (Anderson & Underwood 1997).

Long-term experiment

Initially, the long-term experiment was to be analysed with two-factor ANOVA, but the Kiama site was destroyed in a storm and could not be included in the analysis. To test for the effects of UVR on biomass, number of taxa, and percent cover of algae, at Bass Point, three single-factor ANOVAs were used. All univariate analyses were balanced with five panels from each irradiation treatment. In all cases, data were normally distributed (Shapiro-Wilk, $W > 0.05$) and variances were homogeneous (Cochran's test, $P > 0.05$). Where it was

necessary *a posteriori* comparisons among means were tested with Tukey's HSD.

To test for differences in community structure, percentage cover estimates of taxa on panels were analyzed with non-parametric multivariate techniques. Data for multivariate analysis were fourth-root transformed and Bray-Curtis similarity matrices were calculated (Bray & Curtis 1957). Non-dimensional MDS plots were created to view data in two-dimensional ordinations, and stress levels were less than 0.20. Single-factor NP-MANOVA was then used on Bray-Curtis distances to test for differences in the composition of assemblages among irradiation treatments. The test and the following pair-wise *a posteriori* comparisons among groups were done using the permutation of raw data with 999 permutations (Anderson 2001).

Statistical Software

All univariate analyses were done with JMP v5.0 statistical software. Multivariate analyses were done with the NPMANOVA computer program (Anderson 2001) and nMDS ordinations created with PRIMER v4.0 software (Clarke 1993).

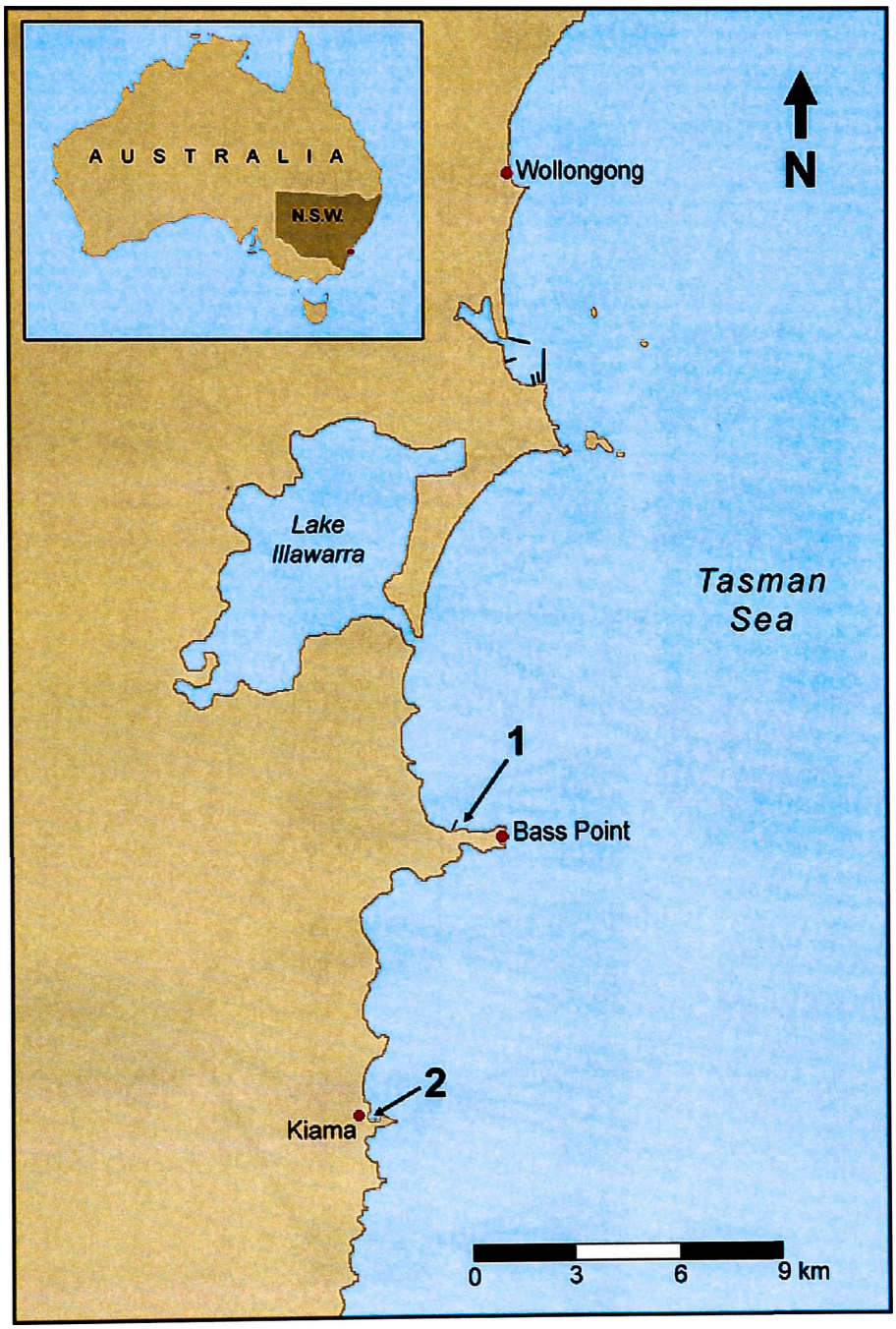


Figure 16. Map of the Illawarra region near Wollongong, Australia, showing the locations of the Bass Point (1) and Kiama Harbour (2) study sites. Red dot in inset map of Australia shows the approximate location of Wollongong.

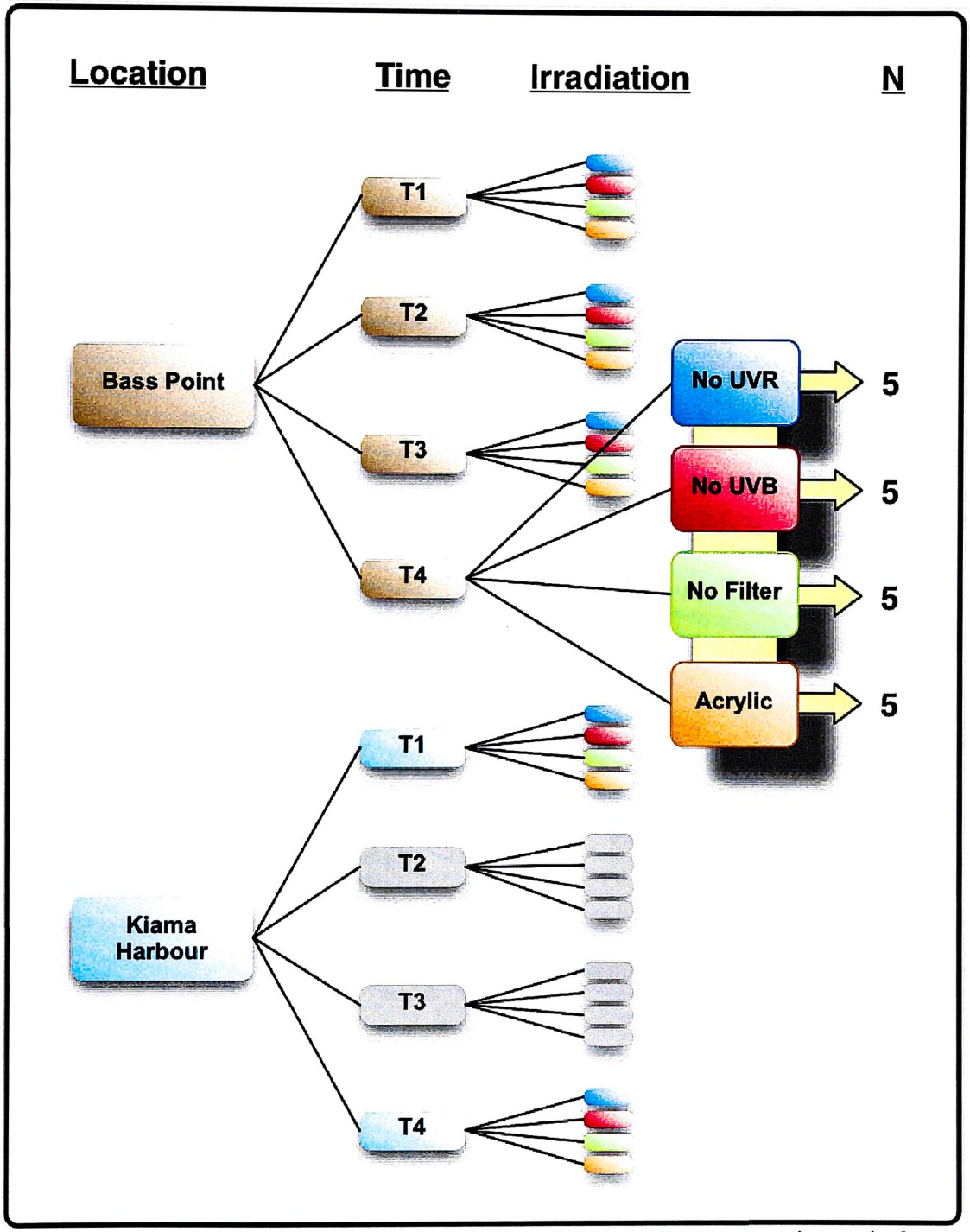


Figure 17. Initial multi-factor ANOVA design of the short-term experiment before a storm destroyed the Kiama Harbour site. The factor "location" (random) had two levels, factor "time" (random) had four levels, and factor "irradiation" (fixed) had 4 levels. There were 5 replicates for each irradiation treatment at each time in both locations. Greyed-out area shows the part of the experiment that was destroyed in the storm.

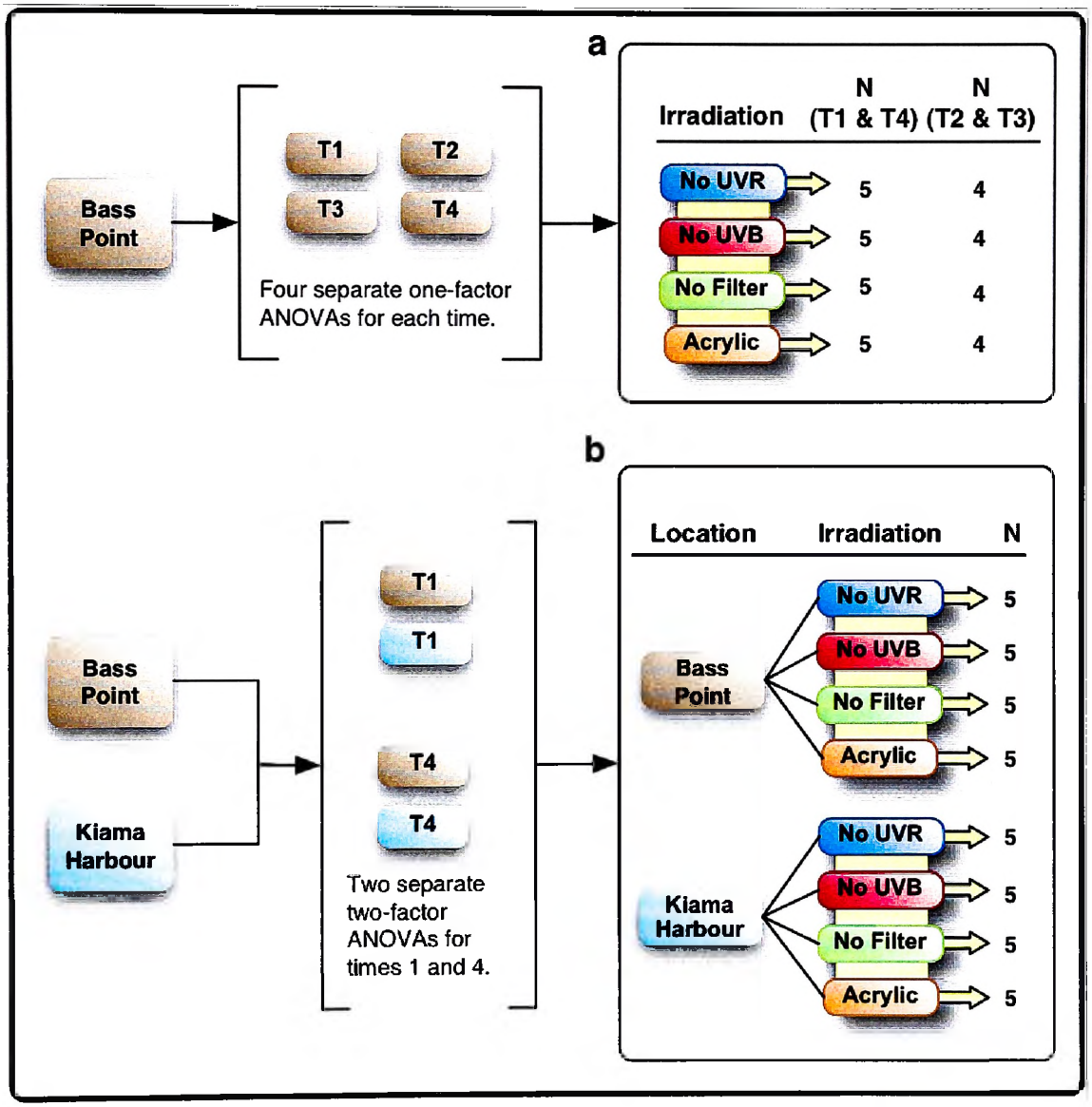


Figure 18. Revised experimental design for the short-term experiment. Because of storm damage the inital experimental design for the short-term experiment had to be broken up into two smaller sets of analyses: (a) Data from Bass Point were analysed with a series of four separate one-factor ANOVAs at times 1 to 4 (N=5 for T1 & T4; N=4 for T2 & T3), and (b) Data from Bass Point and Kiama Harbour were analysed with two separate two-factor ANOVAs at times 1 & 4 only (N=5). The factor "location" (random) had two levels, and factor "irradiation" (fixed) had 4 levels.

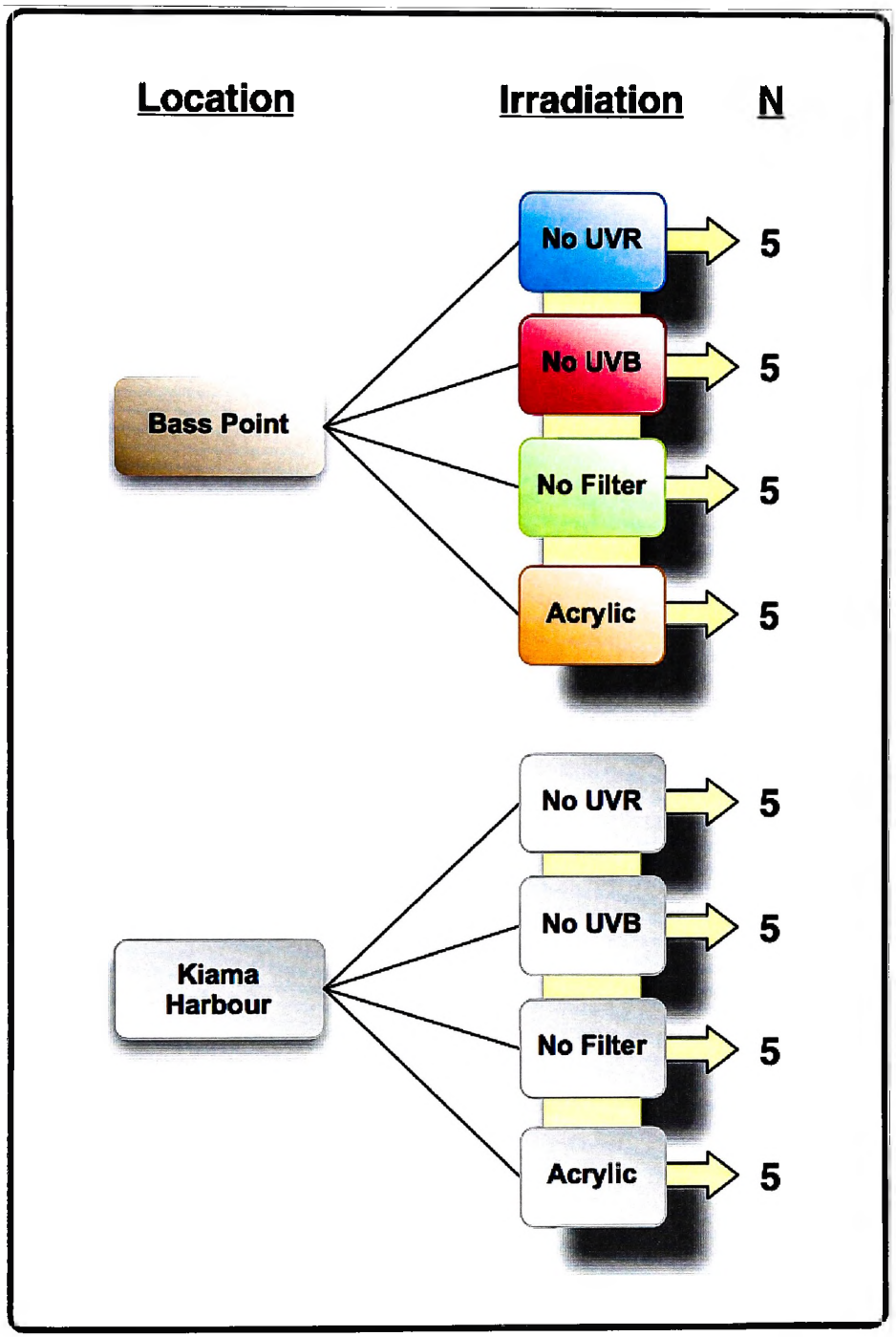
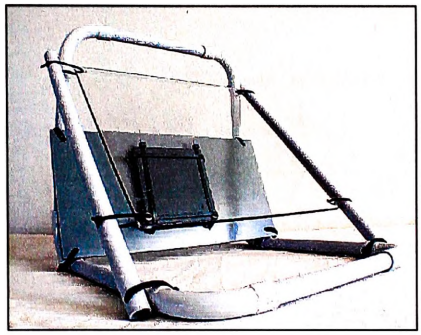
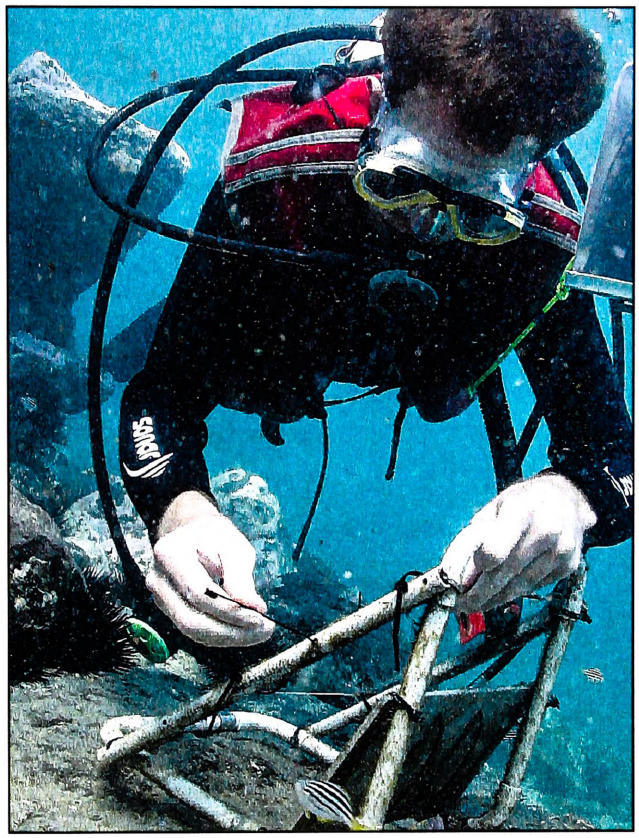


Figure 19. Design layout for the long-term experiment. Initially the long-term experiment was to be anaysed with two-factor ANOVA (Location and Irradiation), but because the Kiama Harbour site (greyed-out) was destroyed in a storm, the revised design for the long-term experiment included only a one-factor ANOVA (Irradiation) on the Bass Point data.

(a) (b)





(c)

(d)

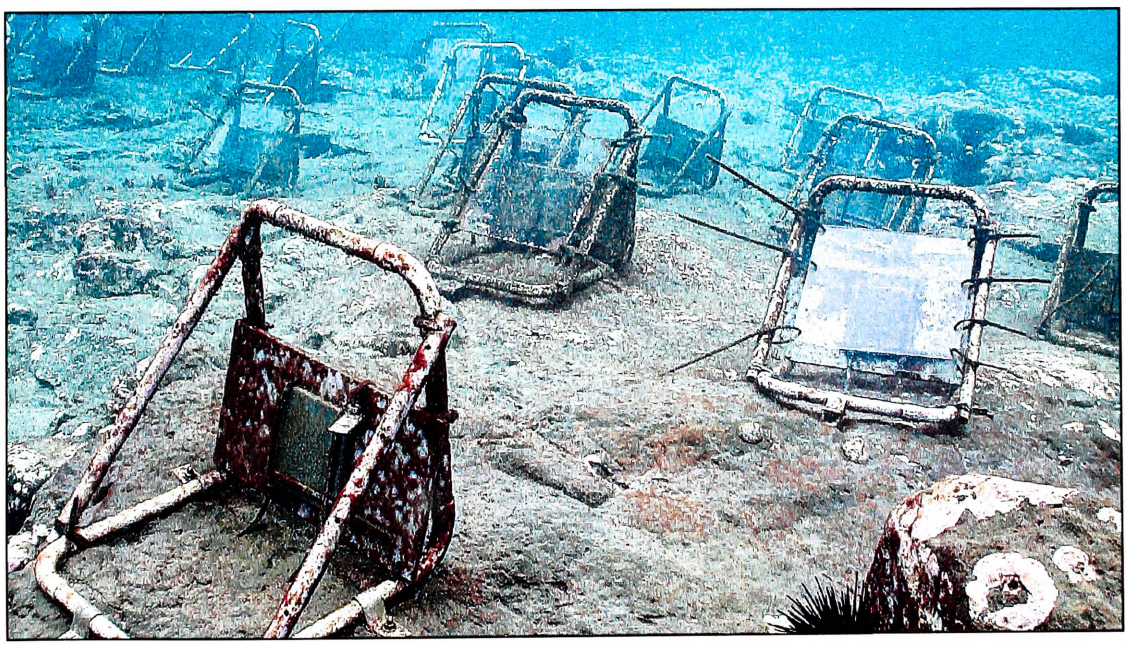


Figure 20. Photos of experimental units used in the field near Wollongong, Australia: (a) assembled unit with filter and experimental panel, (b) a diver cleans a filter and makes repairs to a unit, (c) recently-installed unit without filter and panel, and (d) units at the Bass Point study site.

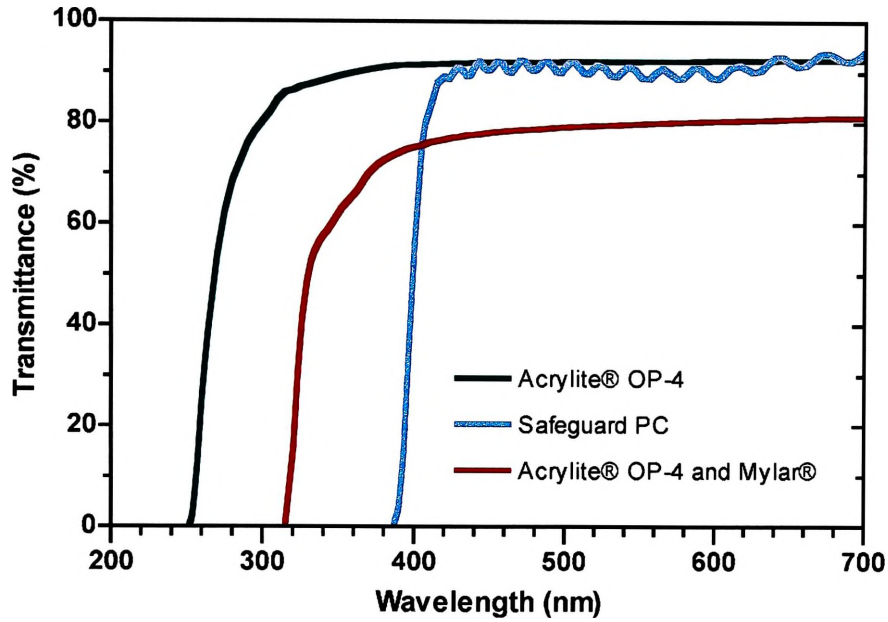


Figure 21. Spectral transmission characteristics of the filter materials used in the experiments near Wollongong, Australia. Transmittance data were collected using a Shimadzu UV-Visible Spectrophotometer (Model #UV-1601; Shimadzu, Australia).

Table 9. The irradiation treatments used in this study and a summary of characteristics of the filter materials used.

Name	Function	Radiation transmitted	Approximate wavelengths transmitted	Filter Materials	Manufacturing information
No UVR	UVR block	PAR[1] only	400-700 nm	Safeguard® Polycarbonate	Tsutsunaka; Tokyo, Japan
No UVB	UVB block	PAR + UVA	320-700 nm	Mylar® & Acrylite® OP-4*	Dupont Teijin Films; Wilmington, DE USA
Acrylic	Control	PAR + UVA + UVB	280-700 nm	Acrylite® OP-4	Cryo Industries; Rockway, NJ USA
No Filter	Control	PAR + UVA + UVB	280-700 nm	-	-

*film was attached to a layer of Acrylite OP-4 ® for structural support

PAR = Photosynthetically Active Radiation

Results

Six major groups of organisms were identified on experimental panels in this study: Foraminifera, Chlorophyta, Phaeophyta, Rhodophyta, Polychaeta, and Crustacea. Out of these six groups 10 distinct taxa were identified and recorded for analyses in this study. Macrobenthic fauna included two unknown varieties of filamentous green algae, one unknown brown alga, and three types of red algae. The red algae consisted of a filamentous type from the family Ceramiaceae, and two others, one encrusting and one branching coralline, from the family Corallinaceae. Macrobenthic flora included two spirorbid polychaetes, *Janua steuri* and *Pileolaria lateralis*, two unknown foram species, and an unknown species of balanoid barnacle. Serpulid polychaetes were also observed on a few tiles; however, because they were extremely rare they were not included in this study.

Short-Term Experiment

Community structure

At Bass Point, there were no apparent effects of irradiation treatments except at time 3. Single-factor NP-MANOVAs done separately for each time showed that assemblages were only significantly different at time 3 (Table 10). Single-factor nMDS ordinations comparing differences among irradiation treatments at each time showed no distinct differences between assemblages except at time 3, where assemblages from the no-UVR treatment were clearly grouped together and

separate from the other three treatments (Figure 22). Pair-wise, *a posteriori* tests confirmed that assemblages under the no UVR treatment were significantly different from the assemblages under the other treatments (Table 10). At Kiama Harbour, NP-MANOVA revealed no significant differences between assemblages at either time 1 or time 4 (Table 11). The nMDs plots comparing differences among irradiation treatments showed no distinct groupings or separation of any of the treatments (Figure 22).

Two-factor NP-MANOVA was used to test for effects of irradiation, location, and the interactive effects between the two factors at times 1 and 4. There was no significant interaction and, as previous tests suggested, there were no significant differences between irradiation treatments at either location. Two-factor nMDS ordinations failed to show clear groupings of irradiation treatments (Figure 23). While there were no significant differences among irradiation treatment, NP-MANOVA did show significant differences between the two locations (Table 12). Time was not a factor in the analysis, but data were included for qualitative comparison.

Number of Taxa

Overall, UVR seemed to have little effect on diversity, as the mean number of taxa observed in assemblages was fairly consistent among irradiation treatments at both locations (Figure 24). At Bass Point, the number of taxa varied slightly among irradiation treatments at each time, however, single-factor ANOVAs done separately for each time revealed a significant treatment effect only at time 3

(Table 13). An *a posteriori* comparison among means (Tukey's HSD) showed that the no-UVB and no-UVR treatments were significantly different.

Data on the number of taxa at Bass Point and Kiama Harbour were also analyzed together at times 1 & 4 with two-factor ANOVA. As expected, analyses showed no significant interaction or treatment effects at either time, but did reveal a significant site effect at time 1 (Table 14). This is because the number of taxa at Kiama Harbour was greater in every irradiation treatment (Figure 24).

Percent cover of algae

At Bass Point, the percent cover of the three algal groups varied among irradiation treatments at all four times (Figure 25), although the effects were only significant at time 2 with the red algal group (ANOVA, $P < 0.05$) (Table 15). Tukey's HSD test revealed a significant difference between the no-UVR and acrylic treatments. No analyses were done for the brown algal group at times 2 and 3, because the data contained mainly zeros in all treatments except the no-UVR treatment. That brown algae were virtually absent from all treatments except the no-UVR treatment indicates that this was a significant treatment effect as well (Figure 25). At Kiama Harbour, there were slight differences among irradiation treatments at time 1 and 4, but like Bass Point at these times, none of these differences was significant.

To test for the effects of irradiation, location, and the interactive effects of these factors on the percent cover of algae, data from Bass Point and Kiama Harbour

were analysed together with two-factor ANOVAs at times 1 and 4. As with the previous analyses, there were no significant irradiation effects at either time. Nor were there significant interactions. There were, however, significant location effects for the green algal group at both times (Table 16). Plots show that percent cover of green algae is more abundant at Bass Point at time 1, but more abundant at Kiama Harbour at time 4 (Figure 25).

Spirorbids

In addition to the multivariate analyses, the two spirorbids, *Pileolaria lateralis* and *Janua steuri*, were also examined with univariate analyses at time 4. The mean number of spirorbids from three $2cm^2$ subsamples on experimental panels was plotted for each species at Bass Point and Kiama Harbour (Figure 26). The mean number of *P. lateralis* was highest under the no-UVR treatment at Bass Point, but at Kiama Harbour it was the lowest. In fact, the effects on *P. lateralis* in all irradiation treatments were virtually opposite at the two locations (Figure 26). As expected, two-factor ANOVA revealed a significant interaction between location and irradiation for *P. lateralis* (Table 17). At Kiama Harbour, the mean number of *J. steuri* was slightly greater than at Bass Point, and varied slightly among irradiation treatments (Figure 26). Two-factor ANOVA revealed that there was a significant difference between locations, however, there was no significant interaction or treatment effect (Table 17).

Assemblage Biomass

Mean biomass of assemblages at Bass Point and Kiama Harbour were plotted at

times 1-4 (Figure 27). At Bass Point, biomass varied among irradiation treatments at all times, however, single-factor ANOVAs done separately for each time revealed no significant irradiation effects at any time (Table 18). Similarly, at Kiama Harbour, there were slight differences in mean biomass among treatments at times 1 and 4, but these were not significant.

At time 1, the effects of irradiation on biomass were similar at both locations, with biomass being higher under the no-UVR and no-UVB treatments than the control treatments (Figure 27). Two-factor ANOVA for time 1, revealed a significant treatment effect, but no significant interaction or location effect (Table 19). An *a posteriori* comparison of the means (Tukey's HSD) showed that only the no-UVB and no-filter treatments were significantly different. At time 4, there were similar variations in biomass under irradiation treatments, but also biomass was considerably higher at Kiama than at Bass Point. A two-factor ANOVA at time 4 showed that there was not an irradiation effect, but there was a significant difference in biomass between locations (Table 19).

Long-Term Experiment

Multivariate analyses in the long-term experiment compared the percentage covers of up to 8 taxa, including two types of green algae, red algae, coralline red algae, spirorbids, two bryozoans, and forams. Unlike the short-term experiment, brown algae and barnacles were very rare and, therefore not included in the long-term analyses.

Community Structure

Analysis of the composition of assemblages with NP-MANOVA revealed significant differences among irradiation treatments (Table 20). An nMDS ordination comparing differences among treatments showed separation and little overlap between assemblages in the no-UVR and the no-filter treatments (Figure 28). There was also separation between the no-UVR and acrylic treatments. Pair-wise, *a posteriori* comparisons among irradiation treatments showed that assemblages from the no-UVR treatment were significantly different from assemblages from the no-filter and acrylic control treatments (Table 20). There was no significant difference between control treatments.

Number of Taxa

The mean number of taxa was highest in the no-filter control (Figure 29). Single-factor ANOVA revealed a significant difference in the number of taxa under different irradiation treatments (Table 21). Among the treatments, however, only the no-UVR and no-filter treatments were significantly different (Tukey's HSD, $P < 0.5$) Athough the number of taxa was slightly higher in the no-filter treatment compared to the acrylic control, there was no significant difference between the two control treatments (Tukey's HSD, $P > 0.05$).

Percent cover of algae

Exploratory analysis of assemblage composition with SIMPER revealed that three algal groups contributed the most to differences among the irradiation treatments.

Further examination revealed that red algae were about 66% more abundant in assemblages under the covered treatments (no-UVR, no-UVB, and acrylic) compared to the no-filter control (Figure 30). One-factor ANOVA showed that the no-filter treatment was significantly different from all the other treatments (Table 22). There was no significant difference between treatments for either of the green algal groups.

Assemblage Biomass

Mean biomass was two or three times higher under the acrylic control than all the other treatments (Figure 31). One-factor ANOVA did not show a significant difference between irradiation treatments (Table 23), however, it was very nearly significant ($P = 0.0833$).

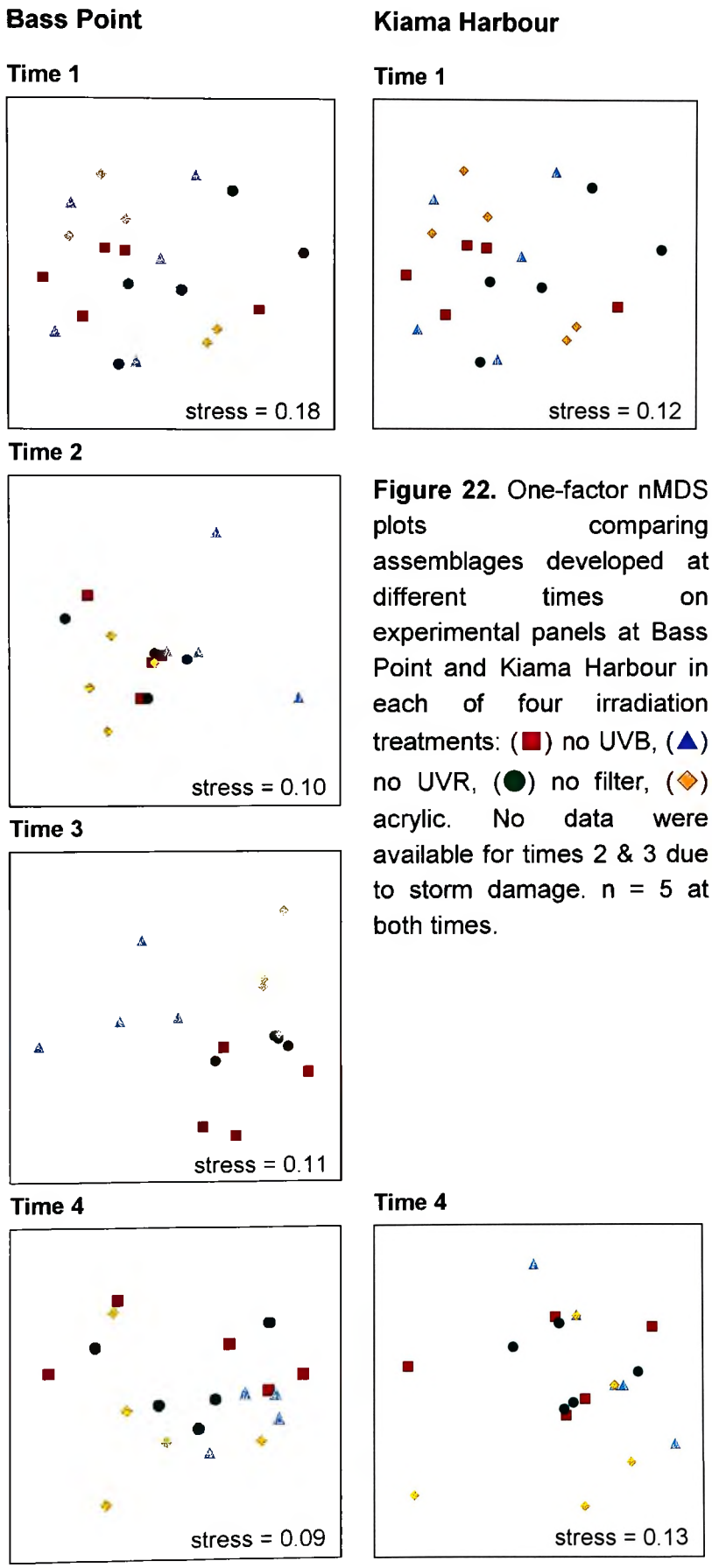


Figure 22. One-factor nMDS plots comparing assemblages developed at different times on experimental panels at Bass Point and Kiama Harbour in each of four irradiation treatments: (■) no UVB, (▲) no UVR, (●) no filter, (◆) acrylic. No data were available for times 2 & 3 due to storm damage. n = 5 at both times.

Table 10. Non-parametric MANOVA on Bray-Curtis distances for assemblages of organisms colonizing experimental panels at Bass Point in each of four irradiation treatments at four different times. Data were fourth-root transformed to reduce the effect of the more common taxa. There were 999 permutations used for all tests.

Source	*Time 1*				*Time 2*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	378.65	1.53	0.171	3	222.87	1.32	0.249
Residual	16	247.87			12	168.94		
Total	19				15			
Source	*Time 3*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	783.37	5.99	0.001	3	93.64	0.40	0.895
Residual	12	130.70			16	231.96		
Total	15				19			
Comparison*							*t*	*P*
No UVB versus No UVR							2.466	0.023
No UVB versus No Filter							1.434	0.202
No UVB versus Acrylic							2.065	0.024
No UVR versus No Filter							3.160	0.027
No UVR versus Acrylic							2.866	0.025
No Filter versus Acryllic							1.952	0.550

*Pair-wise, *a posteriori tests* among irradiation treatments for time 3.

Table 11. Non-parametric MANOVA on Bray-Curtis distances for assemblages of organisms colonizing experimental panels at Kiama Harbour in each of four irradiation treatments at times 1 and 4. Data were fourth-root transformed to reduce the effect of the more common taxa. There were 999 permutations used for all tests.

Source	*Time 1*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	92.11	0.642	0.753	3	97.66	0.773	0.643
Residual	16	143.30			16	126.34		
Total	19				19			

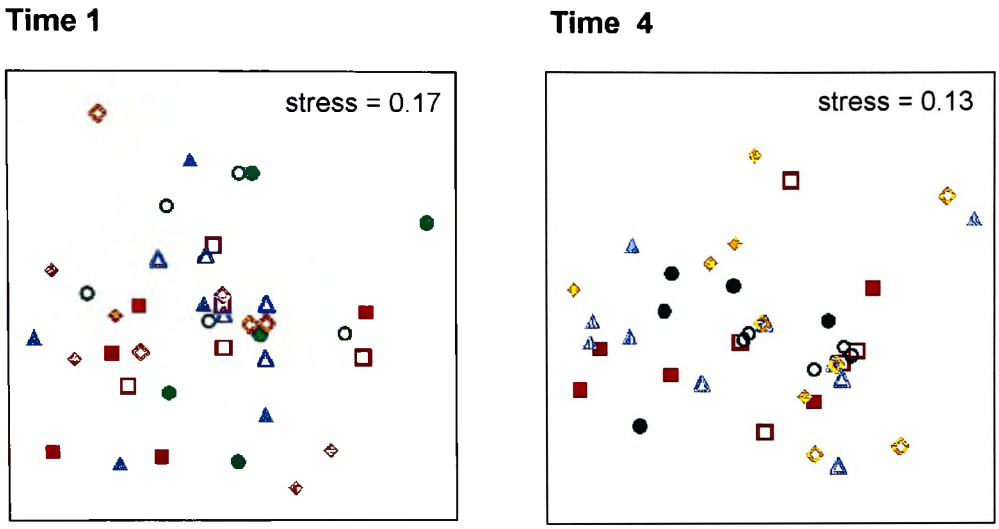


Figure 23. Two-factor nMDS plots comparing assemblages on experimental panels in each of four irradiation treatments at Bass Point and Kiama Harbour at times 1 & 4 in the short-term experiment. Bass Point treatments: (■) no UVB, (▲) no UVR, (●) no filter, (◆) acrylic. Kiama Harbour treatments: (□) no UVB, (△) no UVR, (○) no filter, (◇) acrylic. No data were available for times 2 & 3 due to storm damage. n = 5 for each location at each time.

Table 12. Non-parametric MANOVA on Bray-Curtis distances for assemblages of organisms colonizing experimental panels at Bass Point and Kiama Harbour in each of four irradiation treatments at times 1 and 4. Data were fourth-root transformed to reduce the effect of the more common taxa. There were 999 permutations used for both tests.

Source	*Time 1*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Location	1	859.44	4.39	0.003	1	1919.98	10.72	0.001
Irradiation	3	250.40	1.14	0.441	3	90.82	0.90	0.542
Location × Irradiation	3	220.36	1.13	0.337	3	100.49	0.56	0.799
Residual	32	195.59			32	179.15		
Total	39				39	8226.78		

Table 13. Analyses of number of taxa in assemblages developed on experimental panels at Bass Point in each of four irradiation treatments at four different times with single-factor ANOVA. Variances were homogeneous for each analysis (Cochran's test, P > 0.05). n = 5 for times 1 & 4; n = 4 for times 2 & 3.

Source	*Time 1*				*Time 2*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	0.583	0.86	0.479	3	0.416	0.476	0.704
Residual	16	0.67			12	0.875		
Total	19				15			
Source	*Time 3*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	3.062	3.97	0.035	3	0.983	0.802	0.510
Residual	12	0.770			16	1.225		
Total	15				19			

Table 14. Analyses of number of taxa in assemblages developed on experimental panels in each of four irradiation treatments at Bass Point and Kiama Harbour with two-factor ANOVA. Variances were homogeneous for each analysis (Cochran's test, *P* > 0.05). n = 5 for both times.

Source	*Time 1*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Location	1	48.40	65.60	0.0001	1	0.400	0.492	0.488
Irradiation	3	1.63	2.21	0.1055	3	0.366	0.451	0.718
Location × Irradiation	3	1.00	1.35	0.2738	3	0.666	0.820	0.492
Residual	32	0.73			32	0.812		
Total	39				39			

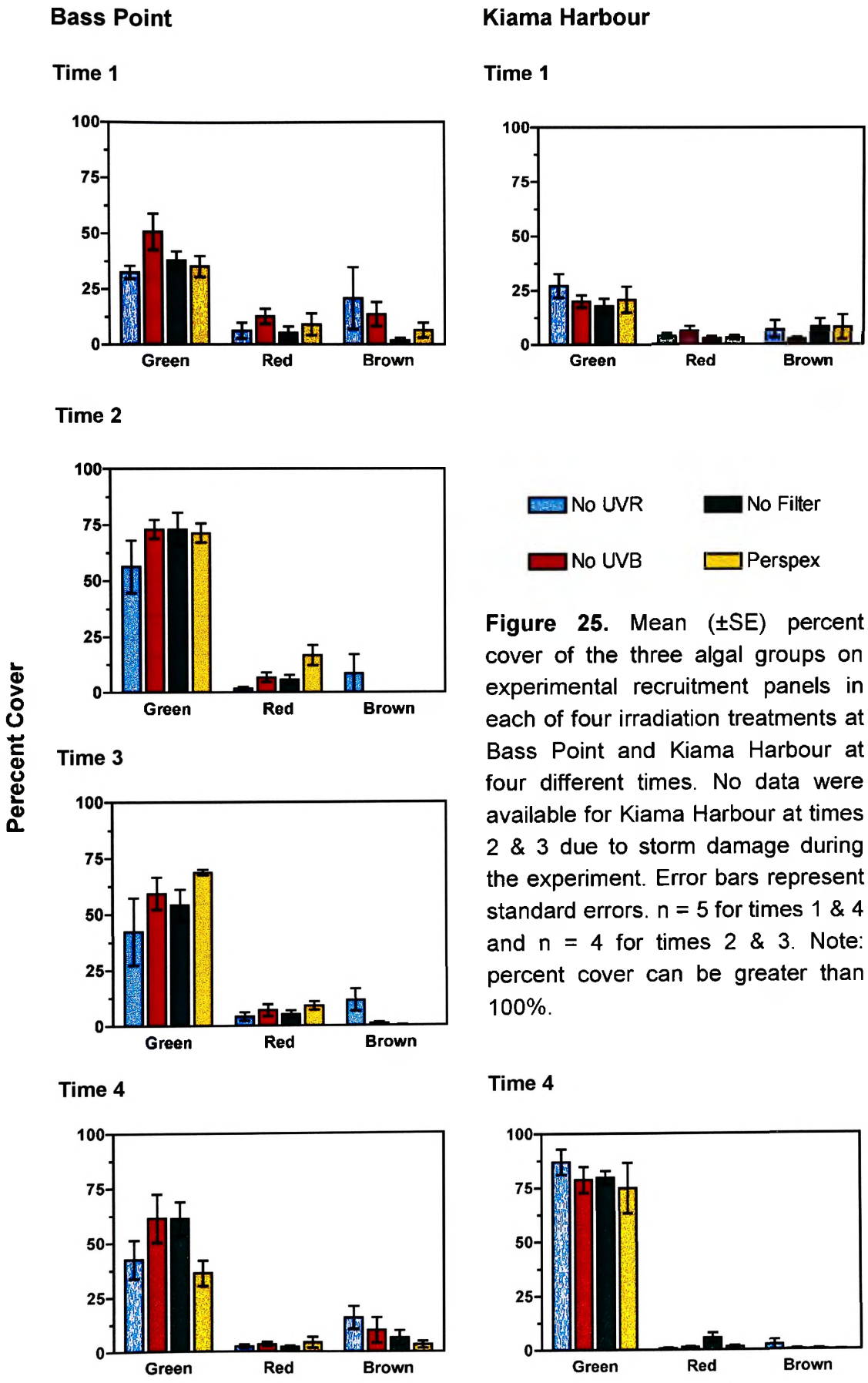


Figure 25. Mean (±SE) percent cover of the three algal groups on experimental recruitment panels in each of four irradiation treatments at Bass Point and Kiama Harbour at four different times. No data were available for Kiama Harbour at times 2 & 3 due to storm damage during the experiment. Error bars represent standard errors. n = 5 for times 1 & 4 and n = 4 for times 2 & 3. Note: percent cover can be greater than 100%.

Table 15. Analyses of percent cover of three groups of algae in assemblages on panels developed at different times at Bass Point in each of four irradiation treatments with single-factor ANOVA. Data for red algae (time 1 & 4) and brown algae (time 1) were log-transformed to correct for non-normality and heteroscedasticity. Data for brown algae at times 2 & 3 consisted mainly of zeros and therefore were not analyzed. Variances were homogeneous for all tests. n = 5 for times 1 & 4; n = 4 for times 2 & 3.

Source	df	*Red*			*Green*			*Brown*		
Time 1		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	0.938	0.69	0.565	325.91	2.30	0.116	5.342	1.007	0.415
Residual	16	1.340			141.70			5.305		
Total	19									
Source	df	*Red*			*Green*			*Brown*		
Time 2		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	156.35	5.35	0.014	264.66	1.14	0.370			
Residual	12	29.18			230.95					
Total	15									
Source	df	*Red*			*Green*			*Brown*		
Time 3		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	17.41	1.01	0.419	484.85	1.48	0.269			
Residual	12	17.12			327.34					
Total	15									
Source	df	*Red*			*Green*			*Brown*		
Time 4		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	0.168	0.26	0.852	833.51	2.26	0.119	58.186	0.614	0.615
Residual	16	0.644			367.50			94.671		
Total	19									

Table 16. Analyses of percent cover of three groups of algae in assemblages on panels developed at different times at Bass Point and Kiama Harbour with two-factor ANOVA. The factor "Irradiation" (fixed) had four levels and the factor "location" (random) had two levels. Data for red and brown algae (time 1) were log-transformed and data at time 4 were arc-sin transformed to correct for non-normality and heteroscedasticity. Data for brown algae at time 4 consisted mainly of zeros and therefore were not analyzed. Variances were homogeneous for all tests. n = 5 for all tests.

Source	df	*Red*			*Green*			*Brown*		
Time 1		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Location	1	1.83	1.81	0.187	3062.5	24.60	0.0001	3.77	1.09	0.30
Irradiation	3	1.28	1.26	0.303	124.0	1.00	0.4054	1.10	0.32	0.80
Location × Irradiation	3	0.12	0.11	0.947	283.3	2.28	0.0977	4.14	1.20	0.32
Residual	32	1.01			124.0			3.43		
Total	39									

Source	df	*Red*			*Green*			*Brown*		
Time 4		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Location	1	0.011	2.26	0.142	1.188	28.16	0.0001			
Irradiation	3	0.004	0.87	0.466	0.050	1.20	0.3243			
Location × Irradiation	3	0.013	2.51	0.076	0.077	1.82	0.1618			
Residual	32	0.005			0.042					
Total	39									

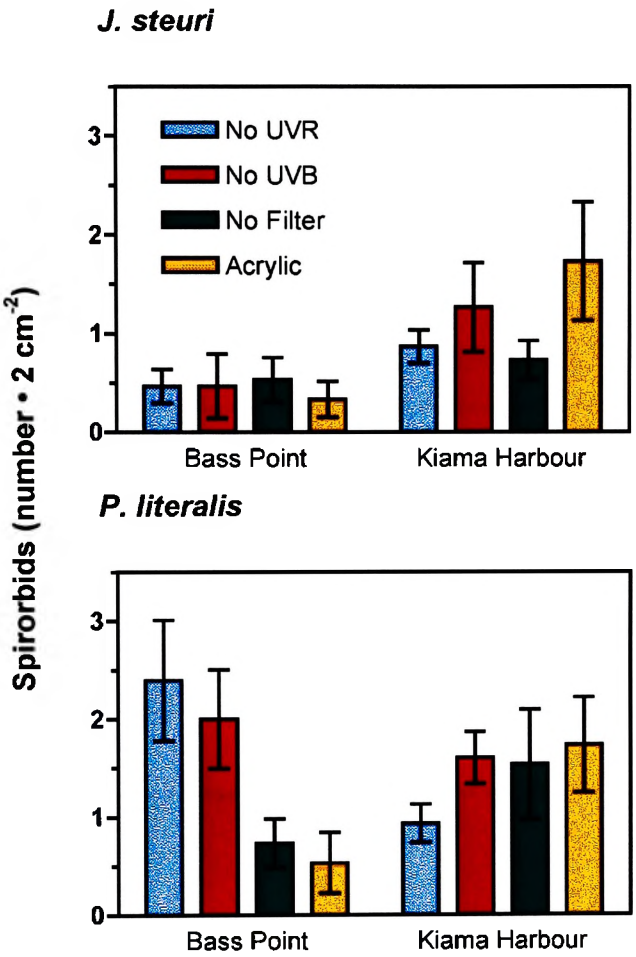


Figure 26. Mean (±SE) number of *J.steuri* and *P. lateralis* on experimental settlement panels in each of four irradiation treatments at Bass Point and Kiama Harbour at time 4. Error bars represent standard errors.

Table 17. Analyses of *P. lateralis* and *J. Steuri* on experimental panels (n = 5) in each of four irradiation treatments at Bass Point and Kiama Harbour with two-factor ANOVA. Factor location had two levels and was random, while factor irradiation had four levels and was fixed. Variances were homogeneous for both analyses (Cochran's test, $P > 0.05$).

Source	*P. lateralis*				*J. steuri*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Location	1	0.011	0.01	0.912	1	4.898	9.209	0.005
Irradiation	3	1.229	1.34	0.275	3	0.346	0.654	0.585
Location × Irradiation	3	3.655	4.01	0.016	3	0.700	1.316	0.286
Residual	32	0.911			32	0.531		
Total	39				39			

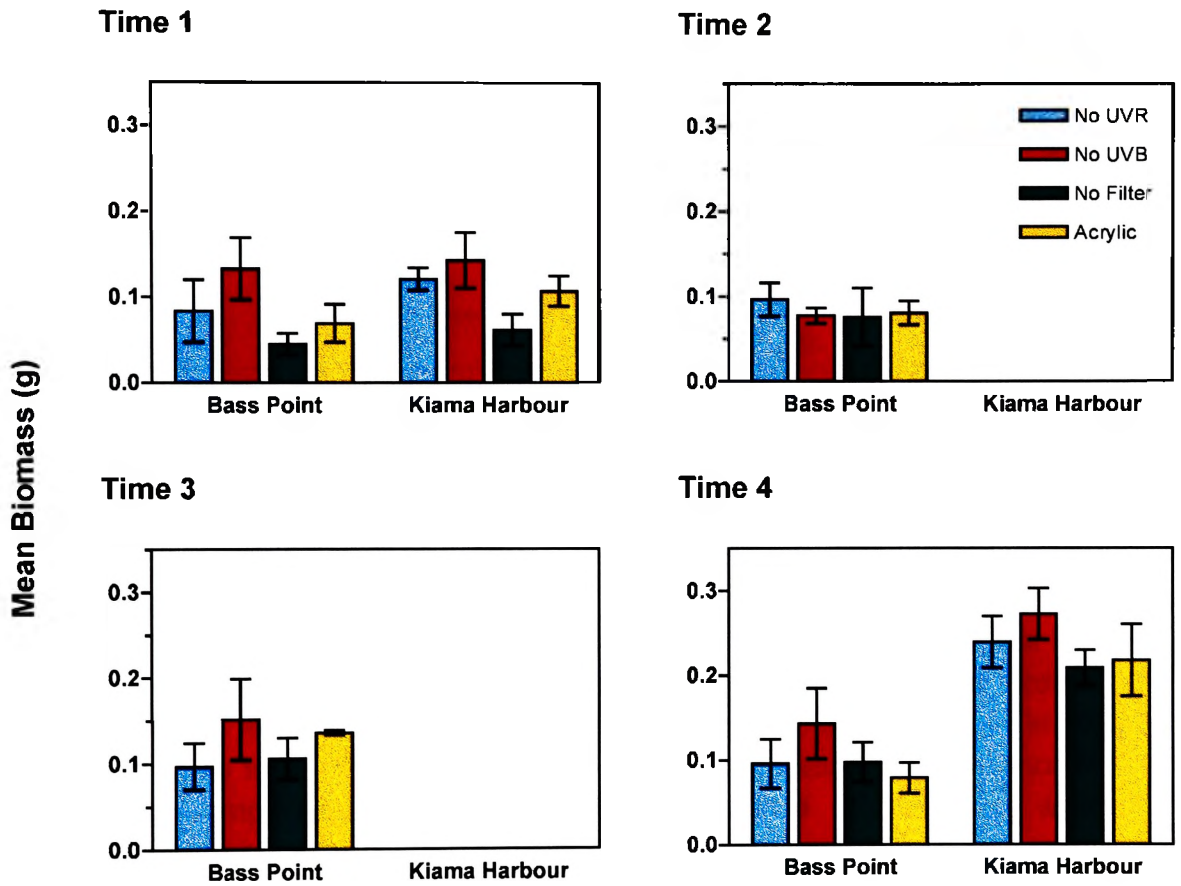


Figure 27. Mean (± SE) biomass of assemblages on experimental panels at Bass Point and Kiama Harbour in each of four irradiation treatments at four different times. No data were available for Kiama Harbour at times 2 & 3 due to losses from storm damage. n = 5 at times 1 & 4; n = 4 at times 2 & 3.

Table 18. Analyses of assemblage biomass on experimental panels at Bass Point in each of four irradiation treatments at four different times with single-factor ANOVA. The degrees of freedom are adjusted for the absence of one sample in the no-filter treatment for time 1. Variances were homogeneous for each analysis (Cochran's test, $P > 0.05$). n = 5 for times 1 & 4; n = 4 for times 2 & 3.

Source	*Time 1*				*Time 2*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	0.0063	1.47	0.263	3	0.0003	0.193	0.899
Residual	15	0.0043			12	0.0018		
Total	18				15			
Source	*Time 3*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Irradiation	3	0.0026	0.73	0.553	3	0.0037	0.867	0.474
Residual	12	0.0036			16	0.0043		
Total	15				19			

Table 19. Analyses of assemblage biomass on experimental panels (n = 5) in each of four irradiation treatments at two locations (Bass Point and Kiama Harbour) at times 1 & 4 with two-factor ANOVA. Factor location had two levels and was random, while factor irradiation had four levels and was fixed. The degrees of freedom are adjusted for the absence of one sample in the no-filter treatment for time 1. Variances were homogeneous for both analyses (Cochran's test, $P > 0.05$).

Source	*Time 1*				*Time 4*			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Location	1	0.0063	1.91	0.177	1	0.1701	35.95	0.0001
Irradiation	3	0.0115	3.49	0.027	3	0.0072	1.53	0.2244
Location × Irradiation	3	0.0005	0.15	0.928	3	0.0005	0.11	0.9541
Residual	31	0.0033			32	0.0047		
Total	38				39			

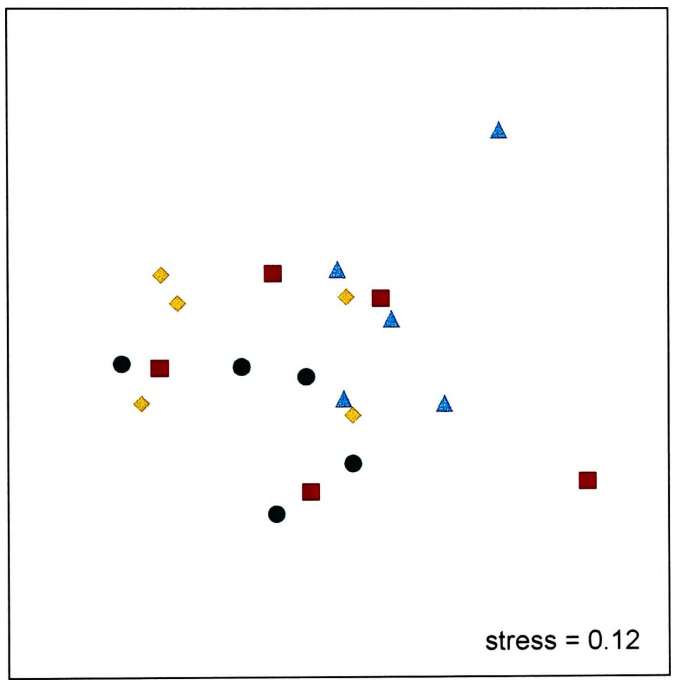


Figure 28. One-factor nMDS comparing assemblages on experimental panels submerged for 84 days in each of four irradiation treatments: (■) no UVB, (▲) no UVR, (●) no filter, and (◆) acrylic.

Table 20. Non-parametric MANOVA on Bray-Curtis distances for assemblages of organisms colonizing experimental panels at Bass Point in each of four irradiation treatments. Data were fourth-root transformed to reduce the effect of the more common taxa. There were 999 permutations used for both tests.

Source	df	SS	MS	*F*	*P*
Irradiation	3	1549.124	516.37	2.14	0.041
Residual	16	3851.946	240.74		
Total	19	5401.070			

Comparison*	t	P
No UVR versus Acrylic	1.7981	0.040
No UVR versus No Filter	2.0546	0.008
No UVR versus No UVB	1.0144	0.423
Acrylic versus No Filter	1.3384	0.165
Acrylic versus No UVB	1.2201	0.319
No Filter versus No UVB	1.3815	0.148

*Pair-wise *a posteriori tests* among irradiation treatments

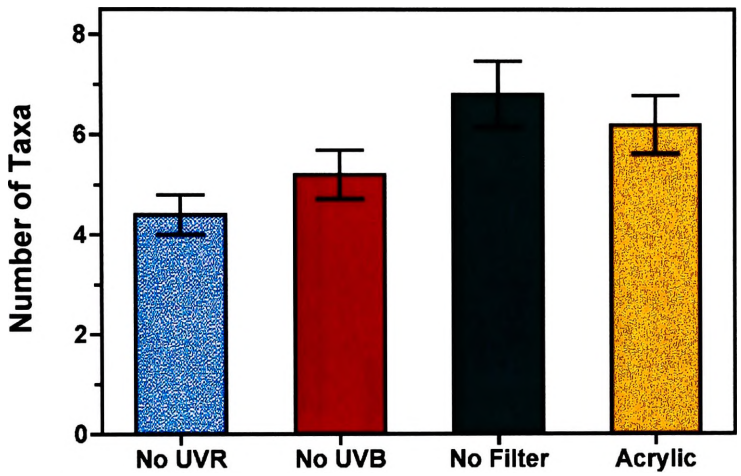


Figure 29. Mean (±SE) number of taxa on experimental panels at Bass Point in each of four irradiation treatments. Error bars represent standard errors.

Table 21. Analysis of number of taxa in assemblages on experimental panels in each of four irradiation treatments with single-factor ANOVA. Variances were homogeneous for each analysis (Cochran's test, $P > 0.05$).

Source	*Number of Taxa*				
	df	SS	MS	*F*	*P*
Irradiation	3	16.95	5.650	3.83	0.030
Residual	16	23.60	1.475		
Total	19	40.55			

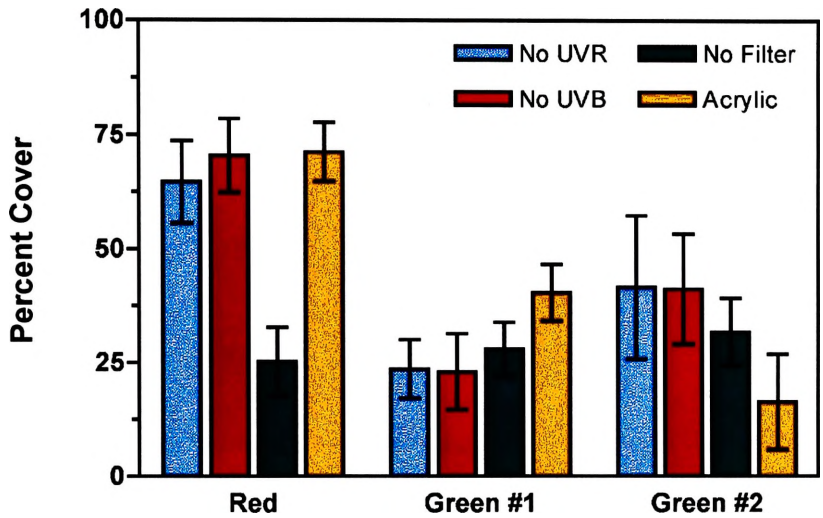


Figure 30. Mean (±SE) percent cover of the three algal groups on experimental panels at Bass Point in each of four irradiation treatments. Error bars represent standard errors.

Table 22. Analyses of percent cover of three algal groups in assemblages on experimental panels in each of four irradiation treatments with single-factor ANOVA. Variances were homogeneous for each analysis (Cochran's test, $P > 0.05$).

Source	df	*Red*			*Green #1*			*Green #2*		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Irradiation	3	2412.2	7.83	0.002	326.5	1.41	0.275	696.58	0.995	0.421
Residual	16	307.8			230.9			700.38		
Total	19									

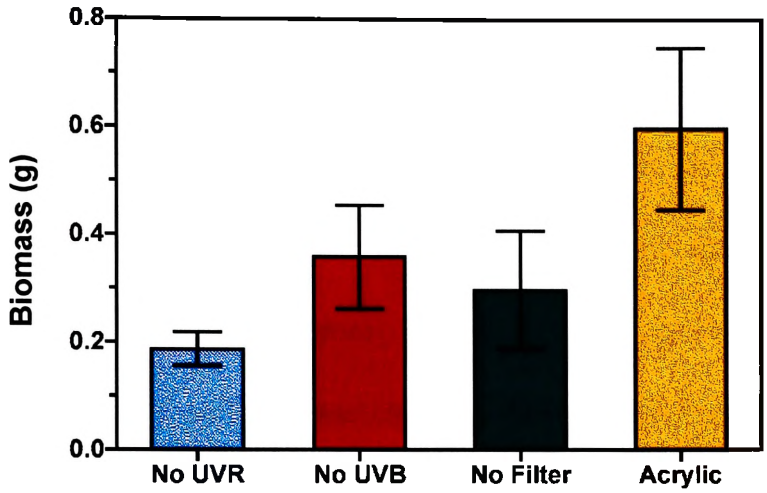


Figure 31. Mean (±SE) biomass of assemblages developed on submerged experimental settlement panels after 84 days at Bass Point in each of four irradiation treatments. Error bars represent standard errors.

Table 23 Analyses of biomass and number of taxa in assemblages on experimental panels in each of four irradiation treatments with single-factor ANOVA. Variances were homogeneous for each analysis (Cochran's test, $P > 0.05$).

Source	*Biomass*				
	df	SS	MS	*F*	*P*
Irradiation	3	0.4494	0.1498	2.66	0.083
Residual	16	0.9004	0.0562		
Total	19	1.3498			

Discussion

Overview

In this study, I investigated the community-level effects of ambient UVR on shallow benthic marine assemblages in temperate Australia with manipulative field experiments using UV cut-off filters. Significant differences in community structure, diversity, biomass, and percent cover of algae were observed among assemblages developed on experimental panels under various irradiation treatments. There were significant differences detected at both short (~19 d) and long time scales (84 d) and at two separate locations, but significant effects were the exception rather than the rule. Furthermore, where significant effects of UVR were detected, they were relatively subtle. In short, while it appears that UVR can have significant community-level impacts on benthic marine assemblages, the detection of significant UV effects was inconsistent (Table 24).

The inconsistency of detected UV effects in this study is not surprising, considering that previous studies on the effects of UVR at the community-level have yielded contradictory outcomes (e.g. Bothwell et al. 1994; Hill et al. 1997; Wullf et al. 1999). The reason for inconsistent UV effects in and among previous studies could be due to one or more of the following: (1) differences in methodological approach, (2) the natural variability of UVR in aquatic ecosystems (due to latitude, weather, depth, turbidity, etc.), or (3) spatial and temporal variability inherent in assemblages (i.e. differences in the type of assemblage at

various times and locations). While the natural variability of UVR and the inherent complexity of natural systems are almost certainly contributing to the inconsistent and subtle effects of UVR in this and previous studies, I contend that the variety of methodological approaches used in previous UV research programs may be limiting the ability to draw general conclusions about the community-level effects of UVR in aquatic systems. Because the outcome of any particular study is dependent on (1) the taxonomic groups that are examined (e.g. trophic levels, see Bothwell et al. 1994), (2) the variables that are measured (e.g. rate variables versus structural variables, see Wulff et al. 1999), (3) the duration of the study (see Wulff et al. 1999, and below), and (4) spatial replication (e.g. this study, see below), it seems plausible that methodological variations could, in part, be responsible for the inconsistency of detected UV effects.

In order to gain a more general understanding of the community-level effects of UVR, I adopted a more comprehensive methodological approach. The strengths of this approach are as follows: (1) manipulative experiments were done in the field using natural UVR, (2) experiments were done at two different time scales and at two locations to increase the generality of the investigation, (3) UVA and UVB were examined concurrently to determine the relative impacts of each spectral bandwidth, and (4) a procedural control (acrylic) was used to test for potential experimental artifacts caused by the use of UV cut-off filters. While some of these methodologies have been used in previous UV research, to my knowledge there is no other study which has incorporated all of these aspects in a

single investigation. Thus, I contend that the findings reported in this study are unique and provide some valuable insight into the role of UVR in marine systems.

For the purposes of this discussion, the key issues that need to be addressed are: the significance of (1) time scale and (2) spatial scales in UV studies, (3) the differential effects of UVA and UVB, and (4) the necessity of proper controls in experiments. Below these issues are discussed in greater detail and in relation to the main findings of this study.

The Importance of Time Scale in UV Studies

Currently, the understanding of the community-level effects of UVR is based primarily on studies that have examined the effects of UV at relatively short time scales (Table 8, page 56). From these studies it is known that significant effects of UVR can occur early in the stages of development (days to weeks), but eventually these effects diminish during later stages of succession (e.g. Santas et al. 1997, 1998a, b; Lotze et al. 2002). For example, Santas et al. (1998b), examined the effects of ambient UVR on tropical diatom assemblages in the Caribbean and found that UVB initially inhibited productivity, but later, as succession proceeded, the harmful effects of UVB on productivity abated. In another study, Santas and others (1997) observed similar effects on the community structure of diatom assemblages in the Mediterranean. Based on studies like these, we might conclude that UV does not have long-lasting effects on benthic assemblages. However, I contend that it would be premature to draw such a conclusion because not enough information is known about effects of UV on benthic

communities at longer time scales.

In this study, one of the most significant findings was that ambient levels of UVR had significant impacts on community structure, not only in the short-term experiment (Figure 22, Time 3, page 80), but also in the long-term experiment (Figure 28, page 92). As mentioned above, numerous studies have reported significant effects of UVR on marine communities in the short term (Table 8, page 56), but the detection of UV effects in the long term is rare. In fact, aside from this study, there is only one other study that has reported significant effects of UVR on communities at long time scales (Wulff et al. 1999). This finding supports the notion that UVR may indeed have significant impacts in benthic assemblages at longer time scales. Nonetheless, it is clear that more field studies examining the effects of UVR at longer time scales are required before we can come to an accurate appraisal of long-term UV effects. Without this knowledge, it is going to be difficult to make predictions about the long-term ecological consequences of UVR in shallow marine environments.

Time scale in UVR studies is important for another reason as well. As has been suggested by Wulff and others (1999), the outcomes of UVR-exclusion experiments are highly dependent on the time scale at which the study was done. For example, in a freshwater study, Kiffney and others (1997), found that the inhibitory effects of UVB on algal biomass and abundance of benthic invertebrates did not occur until the end of the experiment on day 30. Had the study been terminated any sooner, they would not have observed significant UV

effects in their study. As a consequence, they may have erroneously concluded that the UV had no impact. Similar situations are apparent not only in freshwater studies, but also in marine studies (e.g. Cabrera et al. 1997; Santas et al. 1997; Odmark et al. 1998; see Wulff et al. 1999 and references therein). Therefore, it is also important to point out that in addition to examining the effects of UV at longer time scales, it is also necessary to examine the effects at multiple time scales. Otherwise, one might erroneously interpret the outcome of a potentially valuable study and this would certainly not help advance the understanding of the effects of UVR in marine systems.

Spatial Scales of Investigation

While the importance of time scale has been acknowledged in previous studies (e.g Bothwell et al. 1994, Wulff et al. 1999), less is known about the spatial variability in the effects of UVR effects on aquatic communities. As Hill and others (1997) have pointed out, almost all UV experiments (including their own) have been done on small spatial scales. As such, knowledge about the spatial variability of UVR based on previous experiments is limited. This study attempted to examine both the long-term and short-term effects of UVR at a greater spatial scale, by doing experiments at two locations. Despite the damage from storms, it was still possible to compare the effects of UVR at Bass Point and Kiama Harbour for times 1 and 4 in the short-term experiment. While there were many significant effects observed at Bass Point, the only significant effects detected at Kiama

Harbour were on assemblage biomass (Table 24). This demonstrates that the impacts of UVR vary, not only temporally, but spatially as well.

UVB versus UVA

In some community-level studies, it has been demonstrated that UVB can have more of an effect on assemblages than UVA. For example, in a marine study, Wulff and others (1999) used UV cut-off filters to test for the effects of UVR on a meiobenthic community in Sweden. In their study, all significant UV effects that were detected occurred between full-spectrum and UV-excluded treatments, but there were no significant differences between the no-UVR and no-UVB treatments. Thus they concluded that UVB radiation was a significant stress factor for organisms in a microbenthic community and that UVA radiation had no deleterious effects.

Similarly, in this study, there was an instance in which UVB seemed to have more of an impact than UVA. For example, where significant effects of UVR were detected on the biomass of assemblages in the short-term experiment (Figure 27, Time 1), there were significant differences between the no-UVB treatment and the full-spectrum treatment, but no differences between the two UV-exclusion treatments (no UVR and no UVB). As in Wulff and others (1999), this indicates that UVB had more of an impact on the biomass of assemblages than did UVA.

In contrast, however, it is important to point out that UVB does not always have more of an impact than UVA on benthic assemblages. For example, in a freshwater experiment, Bothwell and others (1994), demonstrated that algal

accrual rate increased with the removal of UVA, but no significant effect occurred with the removal of UVB only. Also, In a global UV study (Wahl et al. submitted; see appendix), which examined the impacts of UVR on hard-bottom marine macrobenthic assemblages, Wahl and colleagues discovered that UVB generally appeared to have less of an impact on assemblages than UVA.

Likewise, in this study, there were also instances in which UVA seemed to have more of an impact than UVB. For example, in both the short and long-term experiments the exclusion of both UVA and UVB contributed to greater differences in community structure than did the removal of UVB alone (Figure 22, Time 3; Figure 28). This indicates that it is possible for UVA to have more of an affect on the structure of assemblages that UVB.

In the short-term experiment, I suspect that the reason UVA had more of an impact on assemblages was due mainly to the effects of UVA on brown algae. At times 2 and 3 in the short-term experiment (Bass Point), brown algal cover was present only under the no-UVR treatment, indicating that the brown algal group observed in this study was sensitive to UVA exposure (Figure 25, Times 2 & 3). This effect corresponds well with the nMDS plots of assemblages under the different irradiation treatments (Figure 22, Times 2 & 3). Although significant effects between the no-UVR treatment and the full-spectrum treatment were detected only at time 3, there seems to be a similar pattern at time two.

These findings, which indicate that the brown algae group in this study was sensitive to UVR, is consistent with other studies. Indeed, the sensitivity of brown

algae to UV has been previously reported in a number of species including, *Laminaria solidungala* (Michler et al. 2002), *Ecklonia radiata* (Wood 1997), and *Pilayella littorallis* (Lotze et al. 2002). Furthermore, Michler and others (2002) noted that *L. solidungala* exhibited a reduction in growth, not only when exposed to UVB, but also when exposed to UVA. Thus, I contend that these results demonstrate, that in some cases, UVA can have a greater biological influence on the community structure of benthic marine assemblages than UVB.

In summary, it has been demonstrated that both UVA and UVB can have significant impacts on benthic assemblages in aquatic environments. Therefore, when investigating the community level effects of UVR on benthic marine assemblages, it is important to evaluate not only the impacts of UVB, but also UVA. While it is only the transmission of UVB radiation that is affected by the depletion of stratospheric ozone, UVA radiation still plays a significant biological role. Without distinguishing between the relative effects of both ambient UVA and UVB, it is going to be difficult to make accurate predictions of the consequences of elevated levels of UVB associated with the anthropogenic destruction of the stratospheric ozone layer.

The Importance of Proper Controls

In the majority of cases in which significant UVR effects were found in this study, the procedural (acrylic) and treatment controls (no filter) were not significantly different from each other. This indicates that the presence of filter artifacts in this study (as a result of placing filters over experimental tiles), were not likely, and,

therefore, in this study, the interpretations of the effects of UVR on assemblages are valid, and should not be confounded by the use of filters. There was one instance, however, in the long-term experiment, in which single-factor ANOVA revealed significant differences in the percent cover of red algae among the two controls (Figure 30). In that particular case, the removal of UVR from assemblages appeared to significantly increase the cover of red algae. Taken alone, this suggests that red algae were indeed inhibited by UVR, but because percent cover of red algae was also significantly higher under the acrylic treatment (a covered treatment that mimics the full-spectrum no filter treatment), it is not possible to determine if it was the exclusion of UVR, or the presence of a filter over those treatments that was causing the increase in algal cover. Thus, though it appears that UVR may have had inhibitory effects on red algae, I can not, with certainty, draw this conclusion.

So if the exclusion of UVR from assemblages was not the cause, why would the placement of filters (of varying spectral properties) over these assemblages cause the percent cover of red algae to increase? Although the answer to this question is well beyond the scope of this study, I suspect that the placement of a filter over assemblages may have, like cages, hindered the access of consumers. As a result, red algal cover increased due to the reduced consumer pressure on the algae. For example, the field site at the Bass Point location was occupied by many sea urchins throughout the experiment. Therefore, it is possible that the UV filters hindered access to the treatments with filters limiting them from grazing on those

treatments. As a result, red algal cover increased under the acrylic filters (where urchins did not have access) and red algae decreased under the No Filter treatment (where the urchins had unlimited access to grazing).

While this explanation is speculative, it is worth pointing out that artifacts due to caging have been previously reported in ecological experiments (Kennelly 1991; Steele 1996) and is also the topic of a review (Peterson & Black 1994). How this result compares with previous studies is uncertain. To my knowledge, there are no reports of filter artifacts in any previous ecological study on the effects of UVR. It seems that there could be three explanations for the lack of such information, (1) there truly are no known examples of filter artifacts, (2) filter artifacts exist but have not been published (i.e. bias against papers with negative results or undesirable outcomes), or (3) researchers fail to use methodologies that allow them to test for potential artifacts. Given that the unwanted introduction of artifacts into an experiment are often accidental and unforeseeable, there is always the potential for filter artifacts. Thus, it is the responsibility of researchers to design experiments that will detect, or at least minimize, the potential for this to occur. Nevertheless, there are published studies that lack the use of proper controls (e.g. Santas et al. 1998b).

Conclusion

The objective of this study was to determine the community-level effects of UVR on benthic marine assemblages in temperate Australia. To do this, I chose a comprehensive methodological approach that examined the effects of UVR at

both short and long time scales and at two locations. To my knowledge, this was the first study to examine the community-level effects of UVR on benthic assemblages at both multiple time scales and multiple locations with manipulative field experiments. However, as with previous studies, the findings in this study reveal that the effects of UVR on benthic assemblages are more subtle and transitory, than pronounced and consistent. Whether these findings are due to the complexity of natural systems (e.g. spatial and temporal variability), or the limitations of current methodologies is uncertain. However, as noted in Chapter 2, small sample sizes and high variability among samples in this study may have led to low statistical power. In turn, this may result in the low probability of detecting effects even though real differences among irradiation treatments may be present (i.e. large Type II errors).

Nevertheless, the notion that UVR is capable of producing drastic community-level effects on subtidal benthic assemblages has yet to be demonstrated. As such, it is clear that more rigorous experimental protocols are required. Therefore, I maintain that more experimental field studies, that examine the community-level effects of UVR at multiple time scales and at greater spatial scales are crucial to the understanding of the effects of UVR on benthic marine assemblages. Furthermore, it is imperative that community-level UV studies examine both the effects of UVA and UVB and use proper controls to test for potential artifacts caused by the use of UV-screening filters.

Table 24. Summary of results from the short-term and long-term experiments at Bass Point (BP) and Kiama Harbour (KH): "yes" indicates a significant effect was detected, "no" means there was not. Dash (-) indicates that no data was available due to storm damage.

	Variable	Short-term				Long-term
		T1	T2	T3	T4	
BP	Community Structure	no	no	yes	no	yes
	Diversity (Number of Taxa)	no	no	yes	no	yes
	Biomass	yes	no	no	no	no
	Cover of Algae	no	yes	yes	no	yes
	Spirorbids	-	-	-	yes	-
KH	Community Structure	no	-	-	no	-
	Diversity (Number of Taxa)	no	-	-	no	-
	Biomass	yes	-	-	no	-
	Cover of Algae	no	-	-	no	-

Chapter 4
General Discussion

The sciences do not try to explain, they hardly even try to interpret, they mainly make models.

—John von Neumann

Aims of this Thesis

Here I sought to address a gap in the understanding of the ecological effects of natural UVR on macrobenthic assemblages in the shallow subtidal marine environment. While it is widely known that short-wave UVR is physiologically harmful to individual marine organisms, less is known about the effects that UVR might have on whole communities. Without a clear understanding of how assemblages in natural marine environments respond to ambient levels of UVR, it will be difficult, if not impossible, to make an accurate evaluation of the ecological consequences of elevated levels of UVB caused by stratospheric ozone depletion. Thus, the general aim of this thesis was to assess the responses of benthic marine assemblages to current levels of ambient UVR. This will provide

valuable insight into the role of UVR in marine systems and thereby enable us to make more informed predictions about potential increases in UVB radiation in the future.

More specifically, the main questions addressed in this thesis were (1) What are the community-level effects of natural UVR on shallow-water benthic marine assemblages? That is, does UVR influence community structure, species diversity, and the biomass of assemblages?, (2) Is UVR an abiotic force that can cause structural changes in subtidal benthic marine assemblages? If so, which is more influential—UVB or UVA?, and (3) Are the impacts of UVR general? That is, are the impacts of UVR the same at global spatial scales (e.g. Antarctica and Australia)?

The Main Findings of this Thesis

Given the differential sensitivity of organisms to UVR and the presence of UV in shallow-water, it was expected that the impacts of UVR on the structure, diversity, and biomass of benthic marine assemblages would have been strong and obvious. It was also anticipated that UVB radiation—generally regarded as being more harmful than longer-wave UVR—would have had a greater impact on assemblages than UVA. In contrast to these expectations, I found that (1) the effects of UVR, if they were detected at all, were relatively subtle, and (2) where UV effects were implicated, UVA can sometimes have more of an effect than UVB. In agreement with my expectations, I found that not only do the effects of UVR vary spatially, but also that they vary temporally. Furthermore, it appears

that the effects of UVR on marine benthic assemblages are inconsistent; that is, sometimes they are observable, sometimes they are not. However, this result does not signify that this is due only to the natural variability of UVR in marine systems, and will be discussed in greater detail below.

Overall, despite the geographical and climatological differences in the locations where my research took place, the conclusions drawn from the outcomes of the two studies suggest essentially the same thing: the effects of UVR on benthic assemblages are weak and inconsistent. This, in itself, appears to be a general attribute of UVR in coastal marine benthic communities.

How My Findings Compare with Other UVR Research

Based on recent scientific publications, my research supports previous findings on the community-level impacts of UVR for the following reasons: (1) UV effects are often, but not always, detected at the community-level, (2), when UV effects are detected, they are not always very pronounced, and (3) UVB is not always more detrimental to organisms than UVA. Below, each of these issues is addressed in greater detail.

UV Effects Are Not Always Detected

In support of earlier findings, my research shows that community-level UV effects on benthic assemblages are not always detected. At Casey Station, Antarctica, the findings showed that after a 46-day field experiment there were no discernible effects of UVR on benthic diatom assemblages (Chapter 2). Similarly, in Australia,

depending on the time and location, there were no significant UV effects detected on the structure of the community, biomass, or number of taxa of algal-dominated assemblages (Chapter 3).

This outcome is similar to what others have found in the marine environment. For example, Wulff and others (1999) did a four-month field experiment on a microbenthic community on the west coast of Sweden. Although they measured seven different structural variables (e.g. microalgal biomass and composition, meiofaunal biomass and composition, etc.), they found no significant UVR effects except for ostracodal biomass. Furthermore, as in the Australian study (Chapter 3), these effects did not occur at all points in the study. Similarly, in a freshwater study, Hill and others (1997) reported that they detected no impacts of UVR on periphyton and grazers in a small Tennessee stream. Although, there are some questions about the experimental design and execution of their experiment (see Donahue & Clare 1999), the fact remains that UV effects are not always detected.

Though there are not many published reports that demonstrate a lack of UVR effects at the community-level, it is important to point out that this does not necessarily indicate that the lack of UVR effects is uncommon. The reason for this is that the difficulties in publishing negative results is a continuing problem and is likely to bias the published literature in favor of studies that have detected significant effects.

UV Effects Are Not Always Pronounced

This thesis also supports previous research in the sense that, when detected, UV effects are not always severe or pronounced. Although a few significant effects of UVR benthic marine assemblages in temperate Australia were detected, these cases were usually exceptional and, overall, not severe. This is consistent with other benthic marine studies, which have addressed the effects of UVR at the community-level. For example, Odmark and others (1998) reported significant, but not very strong UV effects on a sand-associated microbenthic community after 2 wks of exposure to enhanced levels of UVB. Similarly, Wulff and others (1999), in a four-month field experiment, detected significant UV effects in a microbenthic community, and noted that these effects were "not very strong".

That UV effects appear to be weak, rather than pronounced, is not extraordinary. In the early days of UV research—especially after the discovery of the Antarctic Ozone Hole in the early 1980s—there was once grave concern that UVR might have the potential to bring about broad-scale ecological devastation. This concern was based primarily on the notion that elevated levels of UVB could have direct impacts on marine phytoplankton and thus have a negative influence on primary productivity (e.g. Worrest 1983; Häder et al. 1985; Häder & Worrest 1991). Such impacts at the base of the food web, it was considered, could be transferred through to the higher trophic levels, thereby causing wide-spread ecological collapse.

In contrast to the early era of UV research, researchers now have more information about the responses of marine communities to UVR in polar (Davidson & Marchant 1994; Davidson et al. 1994; Davidson et al. 1996; Karentz & Bosch 2001; Davidson & Belbin 2002), temperate (e.g. Santas et al. 1997; Odmark et al 1998; Nozais et al. 1999; Wulff et al. 1999; Lotze et al. 2002) and tropical (Santas et al. 1998) regions. Taken together, these studies suggest a more subtle response of communities to UVR. Indeed, in the light of these recent research efforts, it appears that the general paradigm for the ecological impacts of UVR in marine systems is shifting from that of ecological devastation, to one in which the effects of UVR are more subtle (Norris 1999, Karentz & Bosch 2001, Wahl et al. submitted, see appendix). For example, in a review article about UVB in freshwater ecosystems, Williamson (1995) suggested that community responses to UVB are somewhat analogous to other types of anthropogenic disturbance (e.g. acid rain). In these situations, Williamson concluded that while subtle shifts in community structure may be common, overall net ecosystem processes (e.g. primary productivity, nutrient cycling) are mostly unaffected. Similarly, in a review on UVR in Antarctic ecosystems, Karentz & Bosch (2001) concluded that recent evidence of community responses to UVB, indicates that the consequences of ozone depletion in the Antarctic are probably less drastic, but more complex than previously thought.

UVB is Not Always More Influential Than UVA

It seems that there is a generally-held view that short-wave UVB radiation is more biologically-significant than longer-wave UVA radiation. However, as demonstrated in this and other community-level studies, this is not always the case (see Chapter 3).

In my research, UVA significantly reduced the percent cover of brown algae in the short-term experiment in Australia. This is consistent with previous research which shows that UVA is implicated in the reduction of rates of photosynthesis in phytoplankton (Holm-Hansen et al. 1989), inhibition of phytoplankton growth (Jokiel & York 1994; Helbling et al. 1992), mortality in Antarctic bacterial communities (Karentz & Bosch 2001 and references therein), inhibition of freshwater diatom growth (Bothwell et al. 1994), and reduced growth in macroalgae (Michler et al. 2002). Thus, UVA is an important biological factor in aquatic ecosystems.

Because both UVB and UVA can have significant biological impacts, it seems appropriate that studies investigating the community-level effects of UVR should not only examine the effects of UVB, but of UVA as well. Yet despite the clear need to examine both UVB and UVA radiation, UVA has been overlooked in both marine (Keller et al. 1997a, Keller et al. 1997b, Odmark et al. 1998, Nozais et al. 1999) and freshwater (Hill et al. 1997) studies.

General Effects of UVR at the Community-Level

One general pattern that is emerging from recent investigations on the impacts of UVR on benthic assemblages in aquatic environments is that UV effects at the community level are transitory. In the marine environment, the transitory nature of UV effects at the community-level have been documented previously in diatom assemblages in Greece (Santas et al. 1997), diatom assemblages in the Caribbean (Santas et al. 1998b), hard-bottom, benthic communities in Canada (Lotze et al. 2002), and in filamentous algal assemblages in a coral reef mesocosm (Santas et al. 1998a). In freshwater environments, the transient nature of UV effects has been shown in Chironomid-Diatom assemblages in British Columbia (Bothwell et al. 1994), phytoplankton communities in Canadian lakes (Xenopoulos & Schindler 2003), and bacterial communities (Kim & Watanabe 1994). Although the types of assemblages and the methodologies used to study them differed among these studies, the common pattern observed in all was that UV effects diminished over time.

I contend that the findings in this thesis support the notion that the community-level effects of UVR are subtle and transient. However, because I collected only one set of data from each panel (i.e. at collection time), I was not able to obtain data that would allow me to detect changes in assemblages over time. Nevertheless I maintain that the subtle and inconsistent effects of UVR that were observed in my studies, are consistent with the perspective that community-level

UV effects appear to come and go. That being said, why is it that the effects of UVR appear to be transitory?

As Wahl and others (submitted, see appendix) have suggested there are a few models that might account for the transient nature of UV: (1) natural levels of UVR in marine systems vary over time (e.g. seasonal changes), (2) organisms in assemblages acclimate to UVR over time, (3) UV causes a successional shift in the structure of the community from sensitive to more resistant status.

The first possibility (model one), though plausible, is unlikely to have been a factor in the majority of these studies (see references above) for the following reasons: First, most of these studies, including my own, were done during summer when UV levels are highest. In these cases, the intensity of UVR is going to remain relatively high and should not change very much in the short-term. Second, the diminishing effects of UVR do not necessarily coincide with changes in the intensity of UVR. Furthermore, given that most UV studies do not exceed 30 to 40 days, seasonal changes, which occur over longer time spans, are not likely to affect the outcomes of these studies.

The second explanation (model two), which suggests that organisms in an assemblage could acclimate to high levels of UV over time, is also valid. Although our knowledge on the adaptive responses of organisms to UVR are still quite limited, we do know that UV-radiation screening compounds (e.g. mycosporine-like amino acids, MAAs) are utilized by numerous marine organisms as a means of chemical protection from UVR (see reviews Cockell & Knowland

1999; Karentz & Bosch 2001). Furthermore, there is evidence that many of these screening compounds are UV-inducible (Helbling et al. 1996; Drollet et al. 1997; Riegger & Robinson 1997; Cockell & Knowland 1999; Shick et al. 1999). Thus, if organisms are able to respond to the presence of UVR through the acquisition of protective screening compounds, then over time the harmful effects of UV could be mitigated.

While this is a valid explanation for the transient nature of UVR, I do not suspect this model alone can account for these observed patterns. As Wahl and others (submitted) suggested, if the absence of lasting UV effects were due only to UV-induced protection, the lack of significant structural differences between UV treatments would therefore indicate that all organisms in that assemblage were equally capable of adapting. While this may be possible in some situations (e.g. assemblages without UV sensitive species), it does not seem likely, especially since it is understood that the occurrence of UV-absorbing substances varies greatly among species in the marine environment (Karentz 1991). It is clear that more work must be done to gain a better understanding of the ecological role of UV-screening compounds before this model can be completely ruled out. Therefore, of the three, I argue, as do Wahl and others (submittted), that the latter model is most likely to account for the transitory nature of community-level UV effects. This is examined in detail below.

A Conceptual Model for UVR in Marine Systems

As a theoretical component to this thesis, I have endeavored to develop a conceptual model which accounts for the apparent subtle and transitory nature of community-level UV effects on benthic marine assemblages. To do this, I have chosen to employ a successional-based framework from which to structure the model. This model was partly derived from classical successional theory developed by Clements (1916), who popularized a facilitative model of succession whereby early colonists alter the physical environment to make conditions more favorable for later arrivals (Dean & Hurd 1980).

Before the general conceptual model is described in detail, I will first define the term succession as it is used in the context of this discussion. Then, a simple example that demonstrates a commonly-observed pattern caused by full-spectrum solar radiation in marine systems will be presented. Next, a more complex pattern associated with UV treatments (no-UVR and full-spectrum) that are used in a number of community-level UV studies will be described. I will then use this example to explain one possible mechanism whereby the community-level effects of UVR are mitigated over time. Finally, the general conceptual model that I have developed will be presented.

For the purposes of this discussion, succession is best described as the changes in community structure and the composition of species over time (Pickett 1976). In natural communities these changes are brought about by various biotic and

abiotic factors (Greene & Schoener 1982). Thus, ultraviolet radiation is an abiotic factor that has the potential to invoke structural changes in assemblages (Worrest 1983; Williamson 1995; Karentz 1991; Karentz & Bosch 2001).

A contrasting pattern that is commonly observed in the marine environment occurs between areas exposed to full sunlight and adjacent shaded areas (e.g. under piers) (Jokiel 1980; Glasby 1999a, 1999b). In fully-exposed regions the diversity and abundance of sessile invertebrates (e.g. sponges, bryozoans, etc.) are relatively low compared to areas that are shaded (Jokiel 1980). Glasby (1999b) showed that experimental reductions in sunlight by 90% (levels similar to those under piers and pontoons), led to the increased cover of sessile invertebrates (bryozoans, serpulid polychaetes, sponges) and solitary ascidians. In addition to increasing the cover and abundance of "shade-loving" organisms, shading experiments have also shown that the reduction of ambient light reduces the abundance of algal species (Glasby 1999a and references therein).

A simple explanation for this common pattern is as follows: Full-spectrum areas with high amounts of visible light and UVR (e.g. shallow-water benthos), favor the colonization of UV-resistant and phototrophic organisms, but do not favor the colonization of UV-sensitive and shade-loving organisms (Figure 32a). In contrast, fully shaded areas with low amounts of visible light and UVR favor the colonization of UV-sensitive and shade-loving organisms, but not phototrophic organisms (Figure 32b). Therefore, the presence or absence of natural solar radiation in shallow marine environments will ultimately lead to the development

of two distinct communities: one that is dominated by UV-resistant and phototrophic organisms (Figure 32c) and another dominated by shade-loving and UV-sensitive organisms (Figure 32d).

Another commonly-observed pattern in benthic communities is the transitory nature of UVR at the community level (Bothwell et al. 1994; Kim & Watanabe 1994; Santas et al. 1997; Santas et al. 1998a & b; Lotze et al. 2002; Xenopoulos & Schindler 2003; Wahl et al. submitted). Unlike the pattern that was described previously, this one is observed in manipulative field experiments where UVR treatments are created with the use of UV cut-off filters. For the sake of simplicity, two commonly-used treatments will be discussed: (1) a no-UVR treatment in which UVA and UVB are filtered out and only visible light is transmitted, and (2) a full-spectrum treatment that allows the uninhibited transmission of visible, UVA, and UVB radiation. In these experiments, during the early successional phase there is a significant difference in the structure of assemblages under these treatments, but then as succession proceeds, significant differences are not detected. This, in turn, leads to the interpretation that initially there were significant effects of UVR, but that they diminished over time. Hence the conclusion is reached that the effects of UVR at the community level are transitory.

One possible explanation for this pattern is as follows: Similar to the previous example, there are two environments with different light regimes: (1) a full-spectrum environment with high UVR and visible light (Figure 33a), and (2) a no-

UVR environment that is exposed only to high visible light (Figure 33b). Again, in the full-spectrum environment, high amounts of visible light and UVR will favor the colonization of UV-resistant and phototrophic organisms, but will not favor the colonization of UV-sensitive and shade-loving organisms. As in the previous model (Figure 33c), this is going to lead to an assemblage dominated by UV-resistant organisms (Figure 33c). However, at this point, there are two possible ways for an assemblage to develop: either (1) the UV-resistant community dominant is non-facilitative (Figure 33d), or (2) the UV-resistant dominant is facilitative (provides refuge for more UV-sensitive species) (Figure 33e). If the former situation occurs, the outcome will consist of an assemblage that is dominated only by UV-resistant and phototrophic organisms (Figure 33f), but if the latter situation occurs, then the outcome will be an assemblage in which the coexistence of both UV-resistant and UV-sensitive organisms is possible (Figure 33g).

A similar outcome could be observed for the no-UVR light regime (Figure 33b). In this environment the high-visible light favors the existence of phototrophic organisms, while at the same time the absence of UVR favors the existence of UV-sensitive organisms. Ultimately, this might lead to an assemblage that contains both UV-sensitive and UV-resistant species (Figure 33f). Thus, this model demonstrates that it is possible to have similar outcomes for assemblages developing under two different light regimes.

In summary, if the community dominant of a given assemblage is UV-resistant,

than the likelihood of there being a shift in community structure will be minimized because once the UV-resistant species establishes itself, it can then provide a refuge for other UV-sensitive species. Once this has occurred, successional progression of the assemblage can proceed uninhibited by the presence of UVR. Should the UV-resistant community dominant be removed (e.g. by grazing or competition) without another UV-resistant to replace it, then shifts in community structure as a result of UVR are more likely. This model is particularly useful in cases where the community dominant happens to be a canopy-forming species, which can provide refuge for a number of potentially sensitive organisms. Indeed, the protective nature of canopy-forming species has been documented in previous studies (Karsten et al. 1998; Swanson et al. 2000).

To extend this concept further, I will now describe a more general conceptual model that could be useful to describe the impacts of UVR on benthic marine assemblages. According to this model, the relative magnitude of UV effects that are detected in a community-level study are going to be mainly affected by (1) the intensity of UV (i.e. depth), and (2) time. In conjunction, these two factors form a response surface that represents the relative magnitude of UV effects that could be detected in a UV study (Figure 34). Simply stated, the magnitude of UV effects on assemblages will increase where UV intensity is greatest (e.g. summertime, shallow-water) and at shorter time intervals. However, if assemblages can acclimate to the presence of UVR (i.e. through the mechanism described above), then as time progresses the relative magnitude of UV effects decline.

Conclusion

The objective of this thesis was to assess the community-level impacts of solar UVR on subtidal macrobenthic marine assemblages in Antarctica and temperate Australia. Here I sought to address a gap in the understanding of the ecological effects of ambient UVR. In Antarctica, there were no significant effects of UVR on benthic diatom assemblages. In Australia, the effects of UVR on benthic marine assemblages were inconsistent and subtle. These findings are consistent with previous research on benthic communities, which demonstrates that the community-level effects of UVR are subtle and transitory. However, my conclusions should not be interpreted to mean that UVR is unimportant or that it may not cause problems at the community level, for it is clear that UVR can indeed have significant impacts on benthic marine communities and these effects should not be underrated.

Furthermore, it is important to point out that I have only examined the effects of ambient solar radiation by the exclusion of UVR with UV cut-off filters. Thus, it may not be appropriate to extrapolate these results to elevated levels of UVB caused by the anthropogenic destruction of stratospheric ozone depletion. Nonetheless, without a better understanding of the effects of ambient UVR, it will be difficult to make reliable predictions about the ecological consequences of elevated levels of UVR in the marine environment.

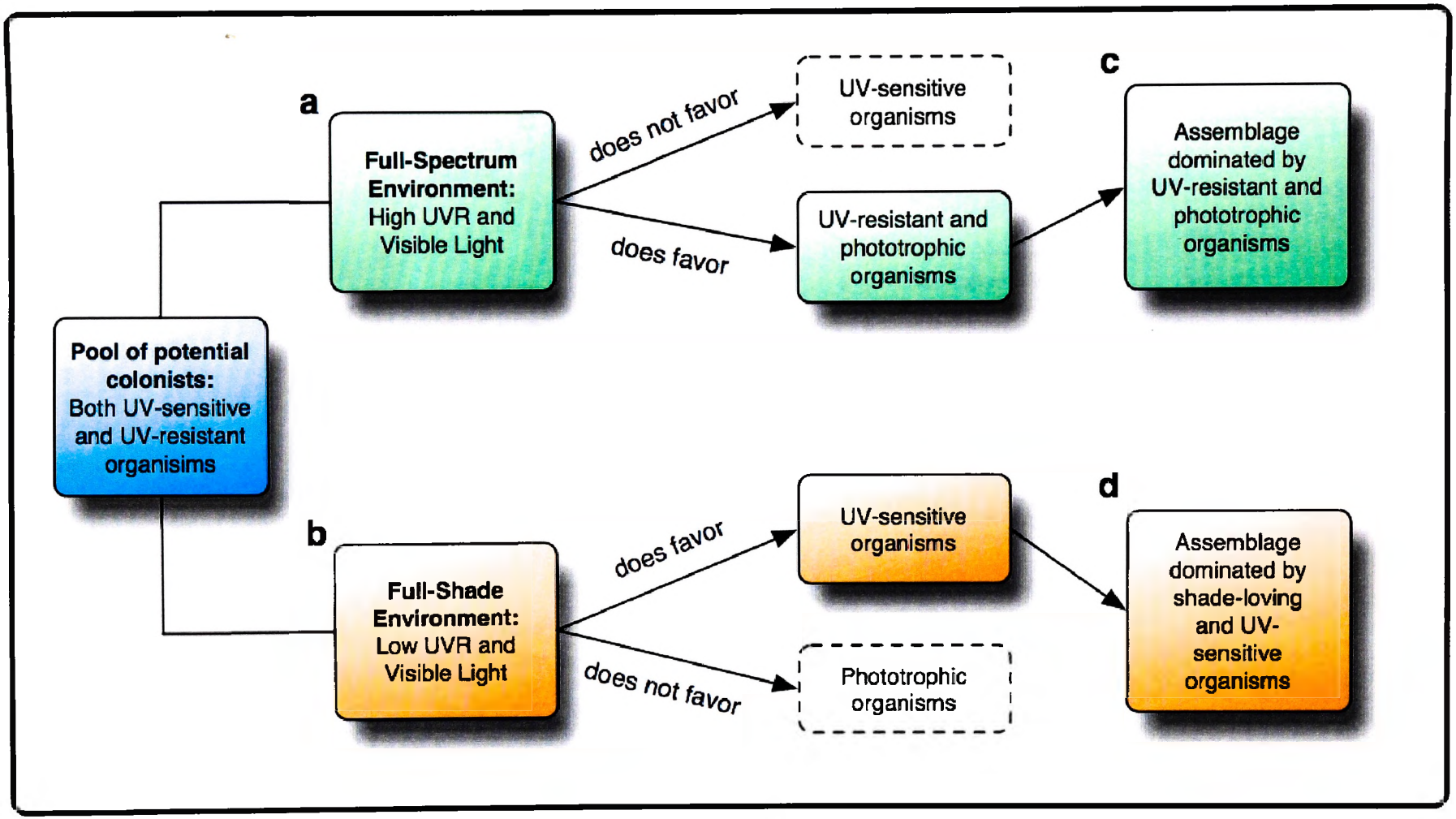


Figure 32. Diagram demonstrating the divergence of assemblages from two extreme light environments: Full-spectrum (a) and Full-shade (b). Full-spectrum environments (green pathway) with high intensities of both UVR and visible light (e.g. exposed shallow-water benthos) are going to favor organisms that are more resistant to UVR and dependent on visible light for photosynthesis (c). In contrast, extreme shaded environments (orange pathway) with low intensities of UVR and visible light (e.g. deep-water benthos, piers, crevices) are going to favor an assemblage dominated by shade-loving and UV-sensitive organisms (d).

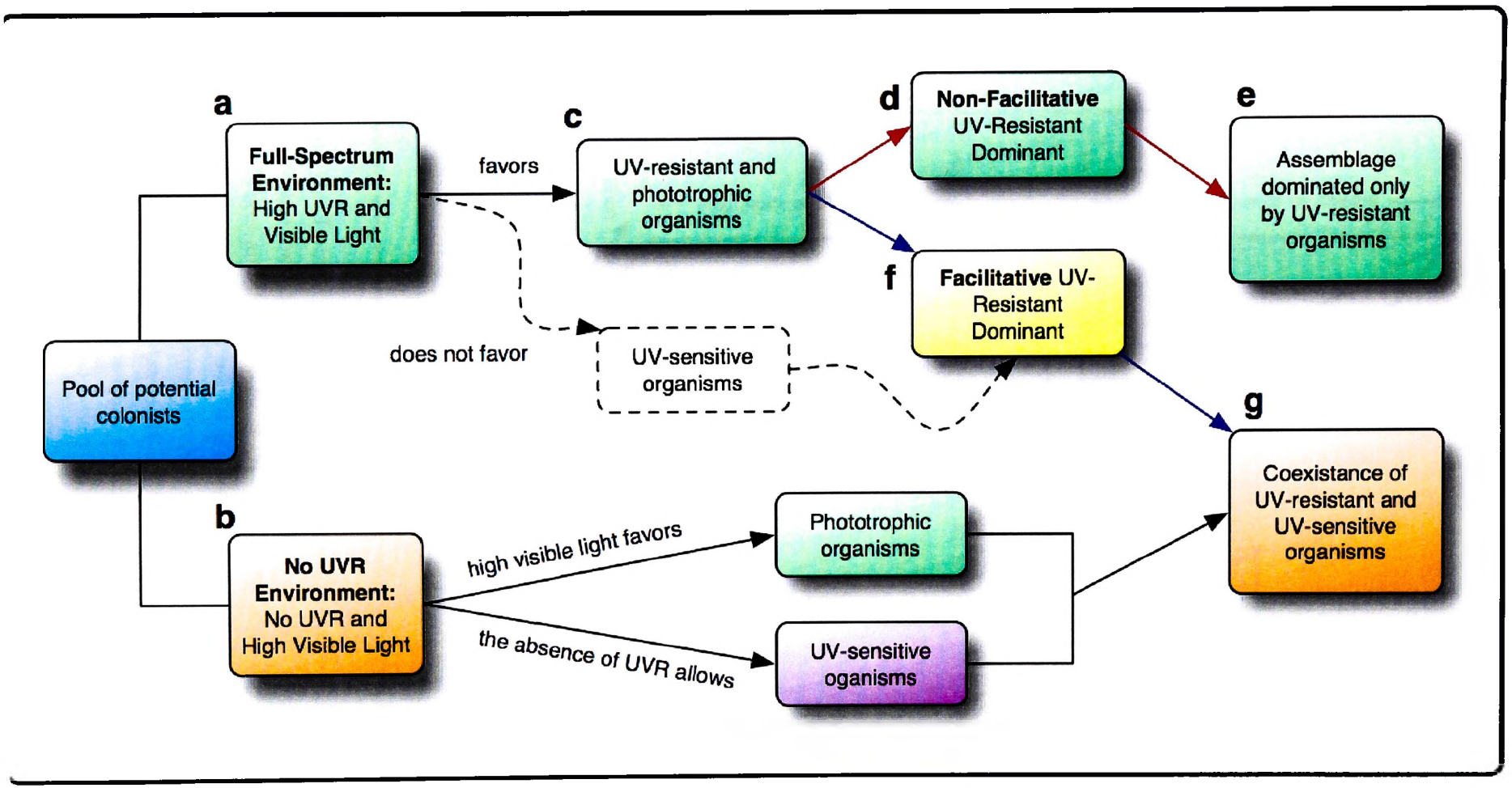


Figure 33. Diagram demonstrating a potential mechanism whereby assemblages from a full-spectrum (a) and no UVR (b) environment can converge. As in the previous example (Figure 29) a high spectrum environment will favor an assemblage that is dominated by UV-resistant and phototrophic organisms (c). However, if an assemblage in a full-spectrum environment contains a non-facilitative UV-resistant dominant (d), then there will be no refuge provided for potential UV-sensitive colonizers and the assemblage will come to be dominated only by UV-resistant species (e). However, if the UV-resistant community dominant is facilitative (f), then there will be a refuge created for UV-sensitive species and therefore UV-resistant and UV-sensitive organisms will be able to coexist in the assemblage (g).

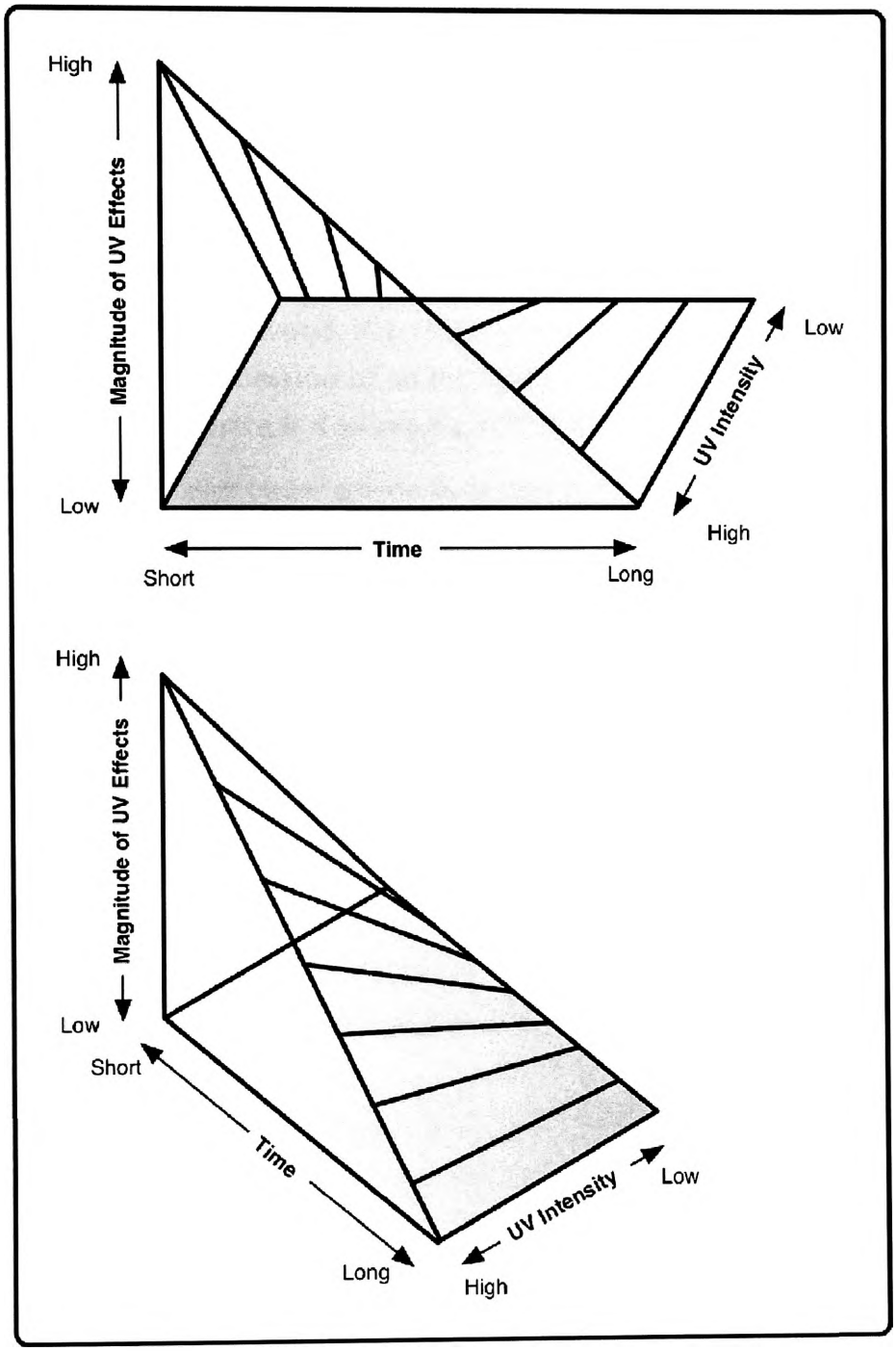


Figure 34. Two perspectives of a basic conceptual model demonstrating the relationship between the relative magnitude of UV effects on benthic assemblages and the intensity of UV (e.g depth) over time. The magnitude of UV effects increases where UV intensity is highest (i.e. shallow-water benthos) and at shorter intervals. Assuming that assemblages can acclimate to UVR (e.g. via a facilitative UV-resistant community dominant), then the magnitude of UV effects is likely to diminish over time.

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APPENDIX

UV effects that come and go: community-level impacts on diversity and biomass in a global comparison

Martin Wahl*, Markus Molis*, Andrew Davis+, Sergey Dobretsov°, Simone T. Dürr*,+, Josefin Johansson§, Jeff Kinley+, David Kirugara&, Matthias Langer^, Heike K. Lotze$, Martin Thiel^, Jeremy Thomason#, Boris Worm$, Dafna Zeevi Ben-Yosef°°

** Mar. Ecol. Sect., Inst.Mar. Sci., Kiel Univ., Kiel, Germany*
+ Dep. Biol. Sc., Univ. Wollongong, Wollongong, Australia
° Dep. Biol. Hongkong Univ. Sci. Technol., Hong Kong, China
§ Dep. Zool. Univ. Tromsoe, Tromsoe, Norway
& Kenya Mar. Fish. Res. Inst., Mombasa, Kenya
^ Fac. Cienc. Mar., Univ. Catolica del Norte, Coquimbo, Chile,
$ Biol. Dep., Dalhousie Univ. Halifax, NS, Canada,
 # School Biol.,Univ. Newcastle, Newcastle upon Tyne, UK
°° Dep. Zool., Tel Aviv Univ. Tel Aviv, Israel

Abstract

Identical field experiments on the influence of ultraviolet radiation on shallow marine hard bottom communities in 10 different coastal regions of both hemispheres produced an unexpected yet consistent pattern: (i) UV impacts species diversity and community biomass in a very similar manner, (ii) UV effects on diversity and biomass were generally weaker than consumer effects, (iii) UVB had less impact than UVA, (iv) ambient UV radiation does not affect the composition of the communities and (v) any UV effects disappeared during species succession. Thus, current levels of UV radiation have small, predictable, and transient effects on benthic communities.

Summary: Current UV levels have little effect on benthic marine communities.

Introduction

The anthropogenic production of ozone depleting substances has led to a reduction of stratospheric ozone concentration and a consequent increase in near-surface UVB radiation (280 - 315 nm) by about 1% p.a. between 1989 and 1997[1]. While the emission of ozone depleting substances is stabilizing or even decreasing, substantial recovery of the ozone layer is not expected before 2050[1]. In the aquatic environment, the UVB-shielding effect of coloured dissolved organic matter (CDOM) is also expected to weaken in the forthcoming decades due to warming and acidification (acid rain over lakes, increased CO_2 input in the oceans), and may lead to further increased exposure of aquatic organisms to UVR.

Past research on UV effects shows a strong bias towards organizational levels at or below the organism, towards microorganisms, plants, and terrestrial environments[4-6]. Studies on the influence of ultraviolet radiation in macrobenthic communities are scarce, regionally focussed and ambiguous in a sense that both presence and absence of negative UV impacts have been demonstrated [7-13].

We may expect UV to affect community structure and diversity if individual species respond unequally to UV radiation with regard to performance or survival. This may happen when some species possess protection against UV while others do not, or when UV protection is metabolically costly. To date, investigations on UV effects on multitrophic benthic community diversity in freshwater or marine habitats give conflicting results[7,9,14-16]. These inconsistencies may stem from the

diversity of approaches among the studies in relation to their taxonomic focus, methodology, or spatial and temporal scale. In order to search for generalities in the response patterns of poorly studied shallow marine hard-bottom communities to UV radiation we scaled up from a local to a global approach. A modular investigation composed of 10 strictly identical and replicated experiments in 10 different biogeographic regions was conducted in 2000/2001. We standardized the experimental set-up for some potentially confounding factors (season, depth, type of radiation, successional phase) but allowed for variability across others (latitude, water parameters, type of community). In order to assess the relative importance of UV impacts, we also manipulated consumer pressure as an experimental reference. These factors were crossed in a factorial design with 6 replicates per site (see Methods). UVA and/or UVB were excluded from the natural irradiation spectrum by selective optical filters. Analogously to consumer exclusion experiments, effects produced by the exclusion of a given factor (consumers, UVB, etc.) are interpreted as the mirror image of the impact of this factor when present. We used factorial meta-analysis and analysis of similarity (ANOSIM) to test (i) whether and how diversity, biomass and community structure of shallow marine hard-bottom communities respond to UV radiation during the first 12 weeks of succession, (ii) whether their response varies among radiation spectra (UVB, UVA, total UV), among community types and/or over time, and (iii) how UV effects relate to and interact with consumption impacts. The 10 experimental sites spanned a wide range with regard to abiotic and biotic

variables. Latitude ranged from 66°S to 68°N, UV irradiation from low (6 W/m^2 UVA, 0.4 W/m^2 UVB) to high (30 W/m^2 UVA, 1.3 W/m^2 UVB), salinity from 15 to 42, temperature from -2°C to 30°C, eutrophication from very low to high, and community type from purely microalgal to functionally diverse.

Results and Discussion

Across the wide range of systems studied, meta-analysis revealed a surprisingly uniform pattern of UV impacts over time both for diversity as for biomass (Fig. 1). Whenever UV effects were significant, they depressed diversity and total biomass. A strong effect, however, seems to be the exception and occurred predominantly in the mid phase of the 12 week succession. Effects were absent at the beginning and at the end of the experiment. The community responses varied between treatments. At no stage during the investigation, did UVB significantly depress diversity or biomass. UVA and total UV transiently reduced both diversity and biomass during mid phase of the experiment. During succession, consumption effects seem to alternate between diversity depressing and diversity enhancing and—in an inverted phase—between biomass enhancing and biomass depressing. However, it was not possible to statistically analyse these effects due to heterogeneity of effect sizes. Strong diversity depressing UV impacts were enhanced by consumption producing a positive interaction effect in mid phase. This was not the case for UV impacts on biomass.

UVB tended to affect diversity less than UVA, but as they both generally acted in the same direction (depressing diversity) their combined action was strongest (Fig. 2). While consumer effects can not be compared directly by meta-analysis (see above) a comparison within site and period revealed that they in most instances were stronger than UV effects with regard to diversity but less so with regard to biomass (73% vs 54% of cases with stronger consumer effects, Fig. 3). During

mid phase succession, when both UVA and total UV showed significant effects, was this tendency reversed. With a single exception (UVB in Norway), community structure was not significantly altered by the treatments applied.

We anticipated shallow water macrobenthic communities to be particularly sensitive to UV radiation during early succession due to the limited attenuation of UV radiation at this depth, the presence of juveniles which tend to be less pigmented or thinner-shelled than adults, and the faster metabolism of juveniles. In addition, in the course of intense (competitive) interactions typical for early stages in species succession UV-stressed species should be more readily excluded from the assemblage.

In contrast to these expectations, UV effects both on the diversity and on biomass of early successional shallow marine hard-bottom communities turned out to be weak, and transitory, and, with regard to diversity at least, weaker than the impact of consumers17. In addition, we did not expect to find that UVB impacted diversity and biomass less than UVA. A similar ranking of UV effects was reported for microalgal communities[16, 18].

The fact that any UV impacts in mid phase disappeared after a few weeks could be due to (i) seasonal changes in UV irradiation, to (ii) an acclimatization response of organisms to UV, or to (iii) a successional or UV-driven shift in community structure to a less sensitive status. The first explanation (model i) seems unlikely since generally maximum effects did not coincide with the seasonal maximum of irradiation. The induction or activation of morphological

or chemical UV protection shields (model ii) on an individual basis has been reported for numerous taxa such as divers microalgal species19,20, macroalgal species and terrestrial plants21, coral larvae22 and vertebrate species[23]. If the observed absence of sustained UV effects were only due to the induction of protection, the absence of any shift in community structure between irradiation regimes would indicate that all species present were equally capable of this kind of adaptation. This seems unlikely. Alternatively, the temporary UV effects may have disappeared due to the proliferation of UV-resistant species (model iii), which after having formed a shading canopy permitted a recovery of the remaining components of the community. Indeed, canopy formation was observed in most sites by pure or mixed stands of the green algae *Enteromorpha spp.* (Australia, China, Chile, Israel) and *Ulvopsis grevillei* (Germany), the red filamentous algae *Ceramium spp.* (Australia, China, Namibia), the brown alga *Chordaria flagelliformis* (Canada) and the blue mussel *Mytilus edulis* (Germany). Protection of understory growth by canopy forming organisms has been observed before[24,25].

Transitory local UV effects on the community level have been reported previously for a filamentous algal assemblage[26], diatom assemblages[16,27], a diatom-invertebrate assemblage[9], and freshwater bacterial and phytoplankton communities[18,28]. The ecological buffering found in the extremely different communities in these studies and the present investigation could be a general feature at this organizational level: single resistant species may provide protection

to others against directional stresses (e.g. UV, currents, sedimentation, abrasion), or more diffuse pressures (e.g. consumption by macrograzers[29]).

In conclusion, deleterious UV effects seem to be smaller in assemblages than described for lower organizational levels. Current levels of UV radiation apparently hardly impact structure, biomass and diversity of coastal benthic communities.

Methods

Identical 2-factorial experiments were run in 10 sites (Namibia [23°S, 15°E], Kenya [4°S, 39.5°E], Chile [30°S, 71°W], Australia [34.5°S. 151°E], Antarctica [66°S, 110.5°E], Canada [44.5°N, 63.5°W], Norway [68°N, 13°E], Germany [54°N, 11°E], China [22°N, 114°E], and Israel [30°N, 35°E]) in their respective summer seasons during 2001 (Fig.4). Experimental units were transparent plastic containers carrying a horizontal settlement tile (70 mm x 70 mm) at a depth of 40 mm below water surface (Fig. 5). Containers were suspended in a float (polystyrol or wood, painted black to avoid reflection of radiation). Macrobiotic communities were allowed to develop over up to 12 weeks on the upper face of the tiles (Table 1). At biweekly to monthly monitoring intervals, the tiles were inspected for successional change and treatment effects with regard to assemblage biomass (tile wet weight minus original tile weight), total cover and percent cover of each species. Two factors were manipulated in factorial combination (Fig. 6). (1) solar radiation was manipulated by cut-off filters above the experimental units on four levels: (a) Perspex (3 mm strong, GS 2648 Röhm, Germany) permitted penetration of the full spectrum (treatment PAR+UVA+UVB), (b) Perspex plus a 0.1 mm polyester transparency film (LTF Nasgua Copy) cut off UVB (treatment PAR + UVA), (c) Makrolon (4 mm strong, LongLifePlus 293, Röhm, Germany) cut off UVA and UVB (treatment PAR), (d) no filter as treatment control). The spectral limits are: PAR = 400 - 700 nm, UVA = 315 - 400 nm, UVB = 280 - 315 nm. (2) consumer pressure was manipulated by either perforating or cutting open widely

the side walls of the containers on three levels: (a) all 4 container walls provided with wide windows to allow consumer access, (b) all walls perforated by holes small enough to excluded local consumers (2-4mm) adding up to an open area equivalent to the windows, (c) cage control [1 wall open, 3 walls perforated]). Access of consumers was manipulated for the 2 extremes of radiation treatment only (PAR+UVA+UVB, PAR). Six replicates were used. Because the optical filters were positioned several cm above the water surface, fouling was not a problem and only spray and bird droppings had to be wiped off regularly. As the treatment controls did not indicate significant treatment artifacts, they were excluded from analysis. Diversity (Shannon Diversity Index H') as computed from species cover (animals and algae) and community biomass were used as response variables. To analyse the effects of different levels of radiation and of consumption and their interaction, a recently developed factorial meta-analysis technique was used[29]. Data were standardized using the meta-analysis metric of standardized effect size, Hedges's d[29]. This is a measure of the difference between experimental and control means, divided by a pooled standard deviation and multiplied by a correction factor to account for small sample sizes. UVB effects were assessed as the difference in diversity or biomass between PAR+UVA+UVB and PAR+UVA treatments, UVA effects as the difference between PAR+UVA and PAR treatments, effects of total UV as the difference between PAR+UVA+UVB and PAR treatments. The graphical representation uses mean effect size + 95% confidence intervals (CI). Non-overlap between CI and zero-line indicates a significant effect,

non-overlap between CIs indicates significantly different effect sizes in different periods. Homogeneity of effect sizes was tested using the Q-statistic[29]. Heterogeneity of effect sizes was detected in the complete data set at several monitoring dates. Homogeneity of the Shannon index was achieved by excluding the 3 most pole-ward sites (Antarctica, Norway, Germany). Homogeneity of wet weights was achieved by excluding monitoring date[3]. But as both exclusions did not change the overall image, for completeness the entire data set is presented in Fig.1, the reduced data set (complying with the all homogeneity criteria) is given in Fig. 7. As the effect sizes for consumption were not normally distributed they were represented by median + percentiles. To compare the relative effects of the different light spectra over the entire experiment, they were ranked within sampling periods and sites, then averaged over periods within sites, and finally the average ranks for each site entered Kruskal-Wallis ANOVA with sites representing the replicates. Differences in community structure were analysed using ANOSIM (Primer® software, Plymouth). The effects of the factors UV, consumption and UV+consumption on community structure were quantified by the dissimilarity indices (ANOSIM R) between treatments and controls. For instance, the difference of community structure expressed as R between a community exposed to PAR+UVA+UVB and a community at the same site exposed to PAR is a proxy for the impact of UV on community structure. Impacts (i.e. R's) were compared by ANOVA after confirming that variances were homogeneous. Average irradiation regimes at the different sites are given in Fig. 8.

Table 1. List of Species composing the communities at the 10 experimental sites.

Antarctica	
Actinocyclus actinochilus	Bacillariophyceae
Achnanthes brevips	Bacillariophyceae
Achnanthes delicatula var.	Bacillariophyceae
Achnanthes c.f. lanceolata	Bacillariophyceae
Asteromphalus hookeri	Bacillariophyceae
Azpeitia tabularis	Bacillariophyceae
Amphora sp. A	Bacillariophyceae
Amphora sp B	Bacillariophyceae
Catacombas camtschatica var. antarctica	Bacillariophyceae
Chaetoceras dicheata	Bacillariophyceae
Chaetoceros socialis	Bacillariophyceae
Cocconeis costata v. costata	Bacillariophyceae
Cocconeis costata v. pennata	Bacillariophyceae
Cocconeis fasciolata	Bacillariophyceae
Cocconeis schuetti	Bacillariophyceae
Coscinodiscus oculus iridus	Bacillariophyceae
Diploneis sp. A	Bacillariophyceae
Diploneis sp. B	Bacillariophyceae
Eucampia antarctica	Bacillariophyceae
Fragilaria striatula	Bacillariophyceae
Fragilariopsis curta	Bacillariophyceae
Fragilariopsis cylindrus	Bacillariophyceae
Fragilariopsis linearis	Bacillariophyceae
Fragilariopsis obliquecostata	Bacillariophyceae
Fragilariopsis pseudonana	Bacillariophyceae
Fragilariopsis kerguelensis	Bacillariophyceae
Fragilariopsis rhombica	Bacillariophyceae
Fragilariopsis ritscheri	Bacillariophyceae
Fragilariopsis sublinearis	Bacillariophyceae
Fragilariopsis vanheurckii	Bacillariophyceae
Gomphonematrophis sp	Bacillariophyceae
Licomorphora sp. A	Bacillariophyceae
Licomorphora sp. B	Bacillariophyceae
Licomorphora sp. C	Bacillariophyceae
Licomorphor decora	Bacillariophyceae
Odontella litigenosa	Bacillariophyceae
Odontella wiesfloggii	Bacillariophyceae
Ophiphora pacifica	Bacillariophyceae
Melosira monoliformis	Bacillariophyceae
Navicula glaciei	Bacillariophyceae
Navicula cancellata	Bacillariophyceae
Navicula directa	Bacillariophyceae
Navicula perminuta	Bacillariophyceae
Navicula sp. A	Bacillariophyceae
Navicula sp. B	Bacillariophyceae
Navicula sp. C	Bacillariophyceae
Nitzschia closterium	Bacillariophyceae
Nitzschia c.f. hybrida	Bacillariophyceae
Nitzschia lecointei	Bacillariophyceae
Nitzschia prolongatoides	Bacillariophyceae
Nitzschia stellata	Bacillariophyceae
Nitzschia subcurvata	Bacillariophyceae
Nitzschia taeniiformis	Bacillariophyceae
Nitzschia sp A	Bacillariophyceae
Nitzschia sp B	Bacillariophyceae
Paralia sol	Bacillariophyceae
Paralia c.f. sulcata	Bacillariophyceae
Pinnularia quadratarea	Bacillariophyceae
Pleurosigma spp.	Bacillariophyceae
Porosira glacialis	Bacillariophyceae
Pseudogomphonema kamtschaticum	Bacillariophyceae
Psudonitzschia lineola	Bacillariophyceae
Psudonitzschia prolongatoides	Bacillariophyceae
Psudonitzschia turgiduloides	Bacillariophyceae
Rhysosolenia sp.	Bacillariophyceae
Stauroneis type species	Bacillariophyceae
Synedropsis fragilis	Bacillariophyceae
Synedropsis c.f. fragilis var A	Bacillariophyceae
Synedropsis hyperborea	Bacillariophyceae
Synedra sp B c.f. fragilis	Bacillariophyceae
Synedropsis c.f. hyperboreoides	Bacillariophyceae
Synedropsis recta	Bacillariophyceae
Synedra sp. A	Bacillariophyceae
Synedra sp C	Bacillariophyceae
Thalassiosira dichotomica	Bacillariophyceae
Thalassiosira gracilis	Bacillariophyceae
Trachyneis aspera	Bacillariophyceae

China	
Perna viridis	Bivalvia
Modiolus comptus	Bivalvia
Anomia chinense	Bivalvia
Enteromorpha	Chlorophyta
Cladophora	Chlorophyta
Ulva	Chlorophyta
Balanus trigonus	Crustacea
Hydroides elegans	Polychaeta
Ceramium sp.	Rhodophyta

Norway	
Mytilus edulis	Bivalvia
Hiatella arctica	Bivalvia
Spongomorpha aeruginosa	Chlorophyta
Cladophora rupestris	Chlorophyta
Balanus balanoides	Crustacea
Diatoms	Bacillariophyceae
Licmophora gracilis	Bacillariophyceae
Bougainvillia ramosa	Hydrozoa
Obelia geniculata	Hydrozoa
Ectocarpus siliculosus	Phaeophyta
Elachista sp.	Phaeophyta
Pilayella littoralis	Phaeophyta
Spongonema tomentosum	Phaeophyta
Fucus sp .	Phaeophyta
Chorda filum	Phaeophyta
Spirorbis spirorbis	Polychaeta

Israel	
Bivalvia Type 1	Bivalvia
Ceracodictyon variabilis	Chlorophyta
Boodlea composita	Chlorophyta
Enteromorpha ramulosa	Chlorophyta
Balanide Type 1	Crustacea
Obelia sp.	Hydrozoa
Steochospermum marginatum	Phaeophyta
Spirorbis sp.	Polychaeta
Ceramium strictum	Rhodophyta
Didemnum sp.	Tunicata

Kenya	
Amphora sp.	Bacillariophyceae
Asterionella sp	Bacillariophyceae
Biddulphia sp.	Bacillariophyceae
Cocconeis sp.	Bacillariophyceae
Coscinodiscus sp.	Bacillariophyceae
Cyanophyte sp.	Bacillariophyceae
Bacillariophyceaetoma sp.	Bacillariophyceae
Dinoflagellate sp.	Bacillariophyceae
Epithemia sp.	Bacillariophyceae
Fragilaria sp.	Bacillariophyceae
Grammatophora sp.	Bacillariophyceae
Licmophora sp.	Bacillariophyceae
Navicula sp	Bacillariophyceae
Nitzchia sp	Bacillariophyceae
Oscillatoria sp.	Bacillariophyceae
Pleurosigma sp.	Bacillariophyceae
Schizothrix sp.	Bacillariophyceae
Spirrullina sp.	Bacillariophyceae
Striatella sp	Bacillariophyceae
Synedra sp.	Bacillariophyceae
Tabellaria sp.	Bacillariophyceae

Germany	
Diatoms spp.	Bacillariophyceae
Melosira sp.	Bacillariophyceae
Mytilus edulis	Bivalvia
Enteromorpha intestinalis	Chlorophyta
Balanus improvisus	Crustacea
Laomedea flexuosa	Hydrozoa
Clava multicornis	Hydrozoa
Pilayella sp.	Phaeophyta
Polydora sp.	Polychaeta
Ceramium sp.	Rhodophyta
Callithamnium sp.	Rhodophyta

Australia	
Watersipora cucullata	Bryozoa
Bryopsis australis	Chlorophyta
Cladophora (1)	Chlorophyta
Cladophora(2)	Chlorophyta
Enteromorpha (1)	Chlorophyta
Enteromorpha(2)	Chlorophyta
Padina	Chlorophyta
Padina(2)	Chlorophyta
Ulva sp.	Chlorophyta
Foraminifera(2)	Foraminifera
Campanulariidae	Hydrozoa
Colpomenia	Phaeophyta
Ectocarpus (1)	Phaeophyta
Ectocarpus(2)	Phaeophyta
Hydroides elegans	Polychaeta
Pileolaria lateralis	Polychaeta
Pomatostegus sp	Polychaeta
branched red alga	Rhodophyta
Ceramium(1)	Rhodophyta
Ceramium(2)	Rhodophyta
Ceramium(3)	Rhodophyta
crustose coralline algae	Rhodophyta
Halocynthia sp	Tunicata
Pyura stolonifera	Tunicata

Chile	
Diatoms (lawn)	Bacillariophyceae
Diatoms (erect)	Bacillariophyceae
Enteromorpha sp.	Chlorophyta
Ulva sp.	Chlorophyta
Cladophora sp.	Chlorophyta
Lepas	Crustacea
Bugula neritina	Hydrozoa
Tubularia sp.	Hydrozoa
Capitella sp.	Polychaeta
Polysiphonia mollis	Rhodophyta
Ciona intestinales	Tunicata

Namibia	
Bivalvia indet.	Bivalvia
Bryozoazoa sp.	Bryozoa
green algal film	Chlorophyta
Codium sp.	Chlorophyta
Cladophora sp.	Chlorophyta
Balanus sp.	Crustacea
Chylocaldia sp.	Rhodophyta
Ceramium sp.	Rhodophyta
Nemastoma lancelatus	Rhodophyta
Centroceras clavulatum	Rhodophyta

Canada	
Mytilus edulis	Bivalvia
Acrosiphonia arcta	Chlorophyta
Enteromorpha intestinalis	Chlorophyta
Ulva lactuca	Chlorophyta
Cladophora rupestris	Chlorophyta
Cladophora albida	Chlorophyta
Chaetomorpha linum	Chlorophyta
Ulothrix flacca	Chlorophyta
Obelia sp.	Hydrozoa
Chordaria flagelliformis	Phaeophyta
Petalonia fascia	Phaeophyta
Pilayella littoralis	Phaeophyta
Ectocarpus fasciculatus	Phaeophyta
Fucus vesiculosus	Phaeophyta
Ceramium nodosum	Rhodophyta
Polysiphonia harveyi	Rhodophyta
Callithamnion tetragonum	Rhodophyta
Bonnemaisonia hamifera	Rhodophyta
Cystoclonium purpureum	Rhodophyta
Dumontia contorta	Rhodophyta

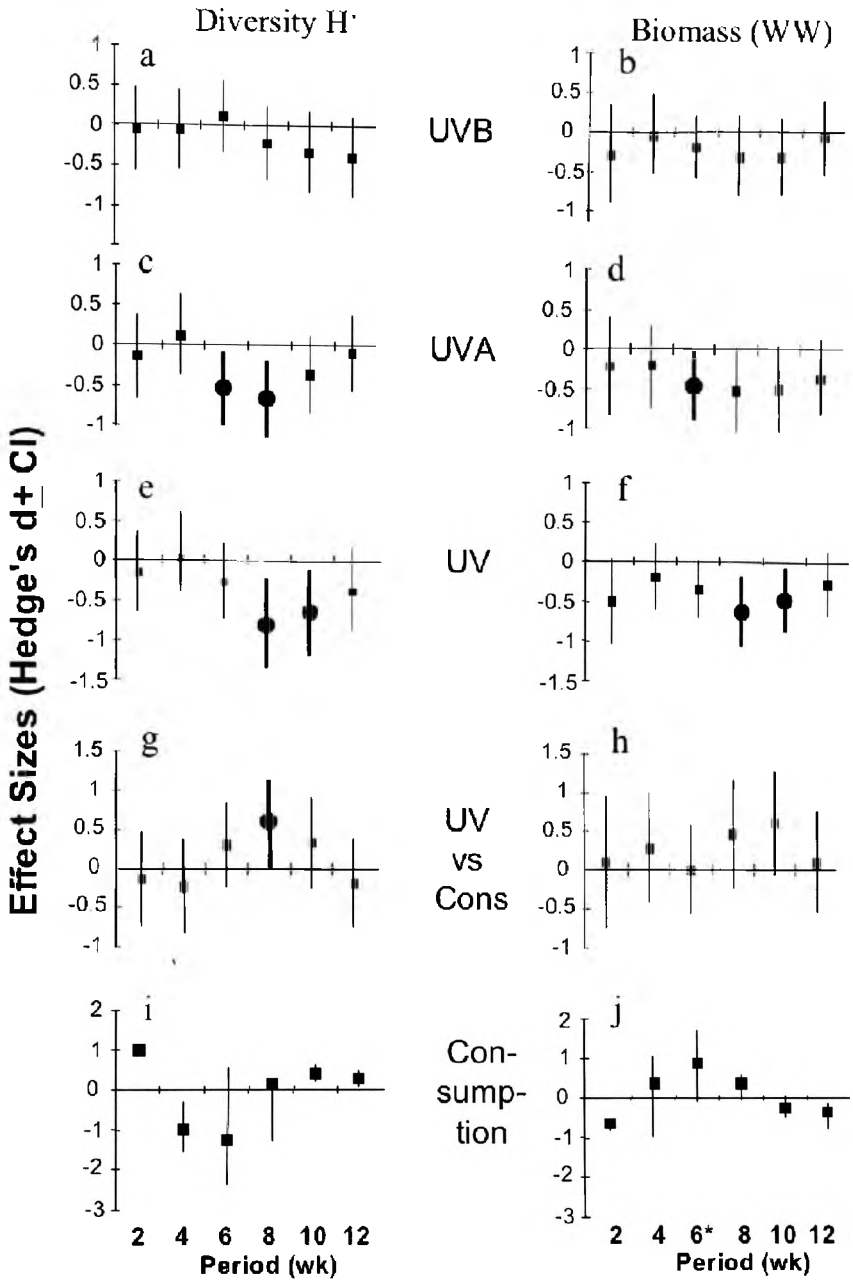

Figure 1. Impacts of UV and consumption on species diversity (left column) and community biomass (wet weight, right column). Shown are the mean effect sizes (Hedges's d, 95% CI) as obtained by factorial metaanalysis of UV radiation and consumer pressure on the diversity of benthic communities in the course of a 12 week succession. Hedges's d linearily relates to a % change in diversity (H') as d = 3.63*H'. Thus, a d of -1 represents a treatment-driven decrease in diversity H' by 27.5%. Non-overlapping CIs indicate significant differences (P<0.05). Although some sites and some periods caused heterogeneities, for completeness the entire data set is presented here. Omitting the heterogeneity-causing sites and periods does not change the overall picture as can be seen in fig. 7. Effects of UVB (a, b), UVA (c, d), total UV (e, f), interaction between total UV and consumption (g, h) and effects of consumption (i, j).

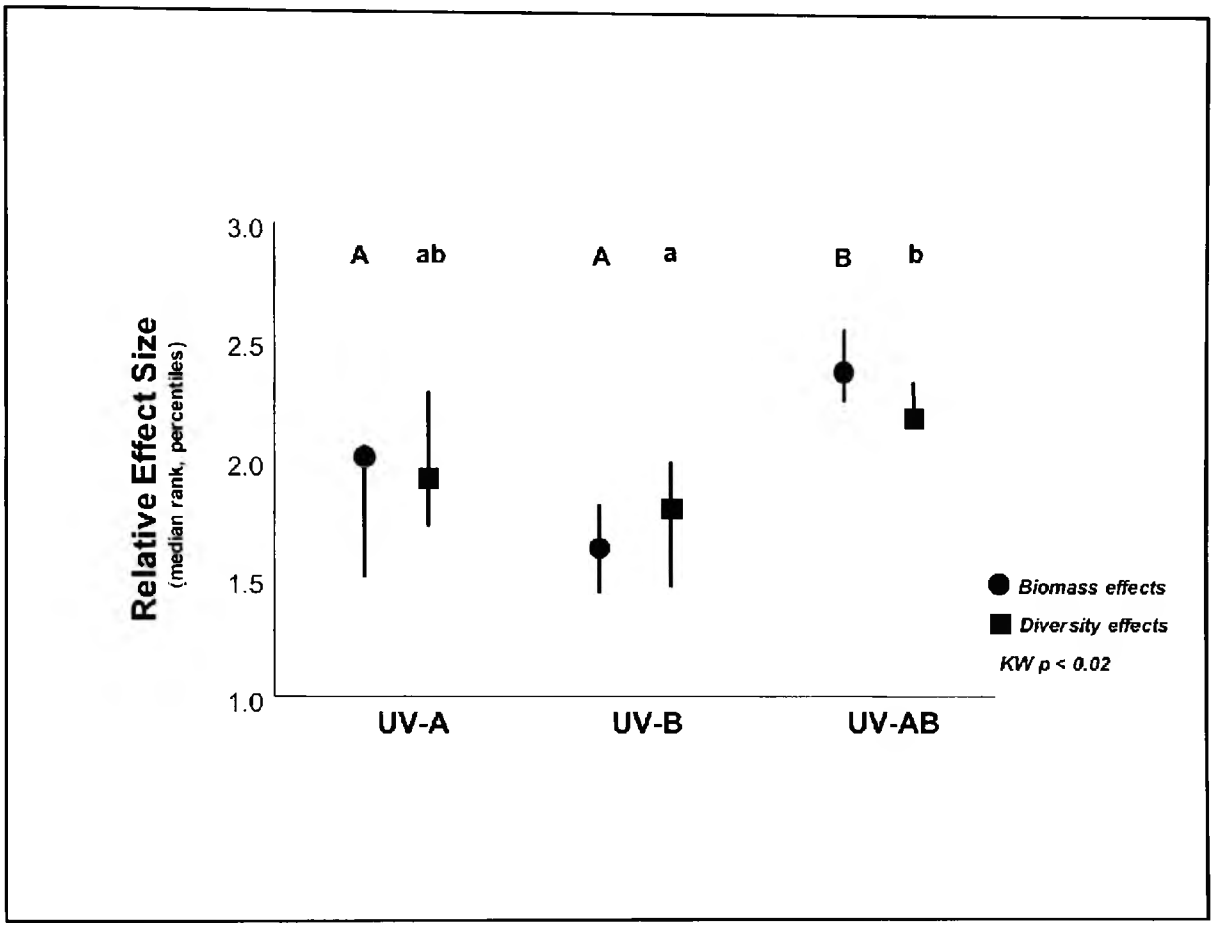

Figure 2. Relative effects of UVA, UVB and total UV on species diversity (squares) and community biomass (dots) (median, percentiles). UVA tends to reduce diversity and biomass more strongly than UVB. Treatments sharing a letter in the top row do not differ significantly (uppercase letters for biomass, lower case letters for diversity). KW: Kruskal Wallis ANOVA.

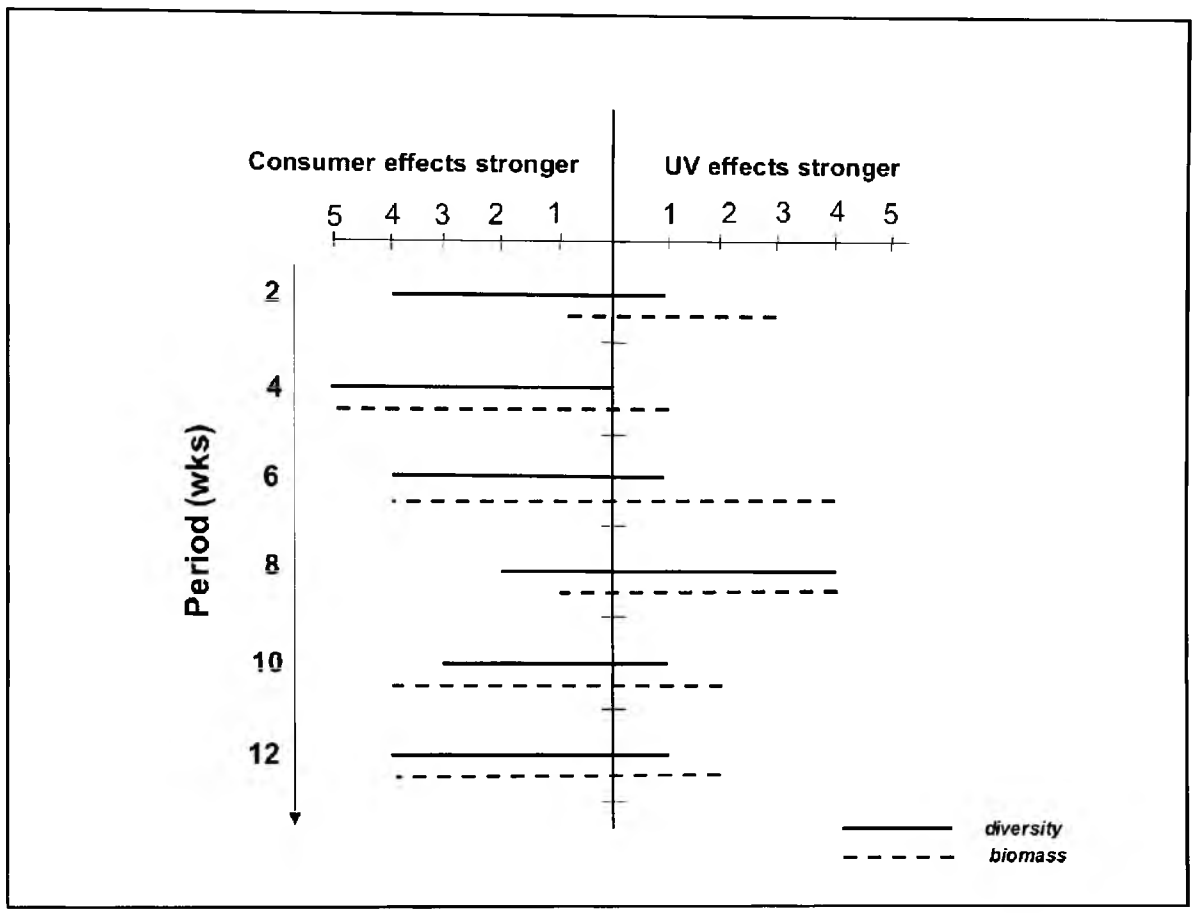

Figure 3. Local importance of consumption versus total UV radiation: Number of sites where consumer effects on diversity (complete lines) and biomass (dotted lines) were stronger than UV effects (bars to the left) or where UV effects were stronger than consumer effects (bars to the right) in specific periods of the succession. Consumer effects on both variables tend to be stronger except during the mid phase of succession.

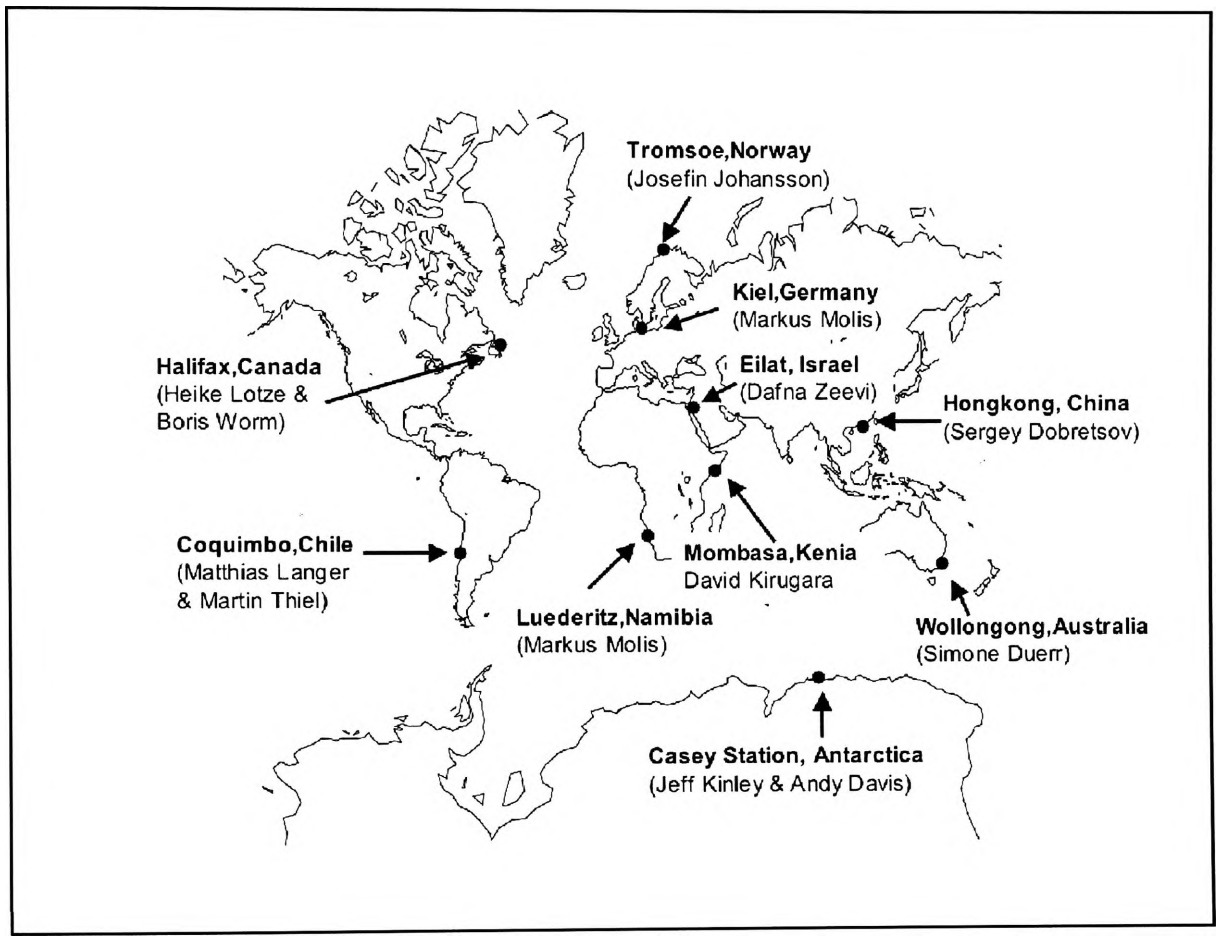

Figure 4. Experimental sites.

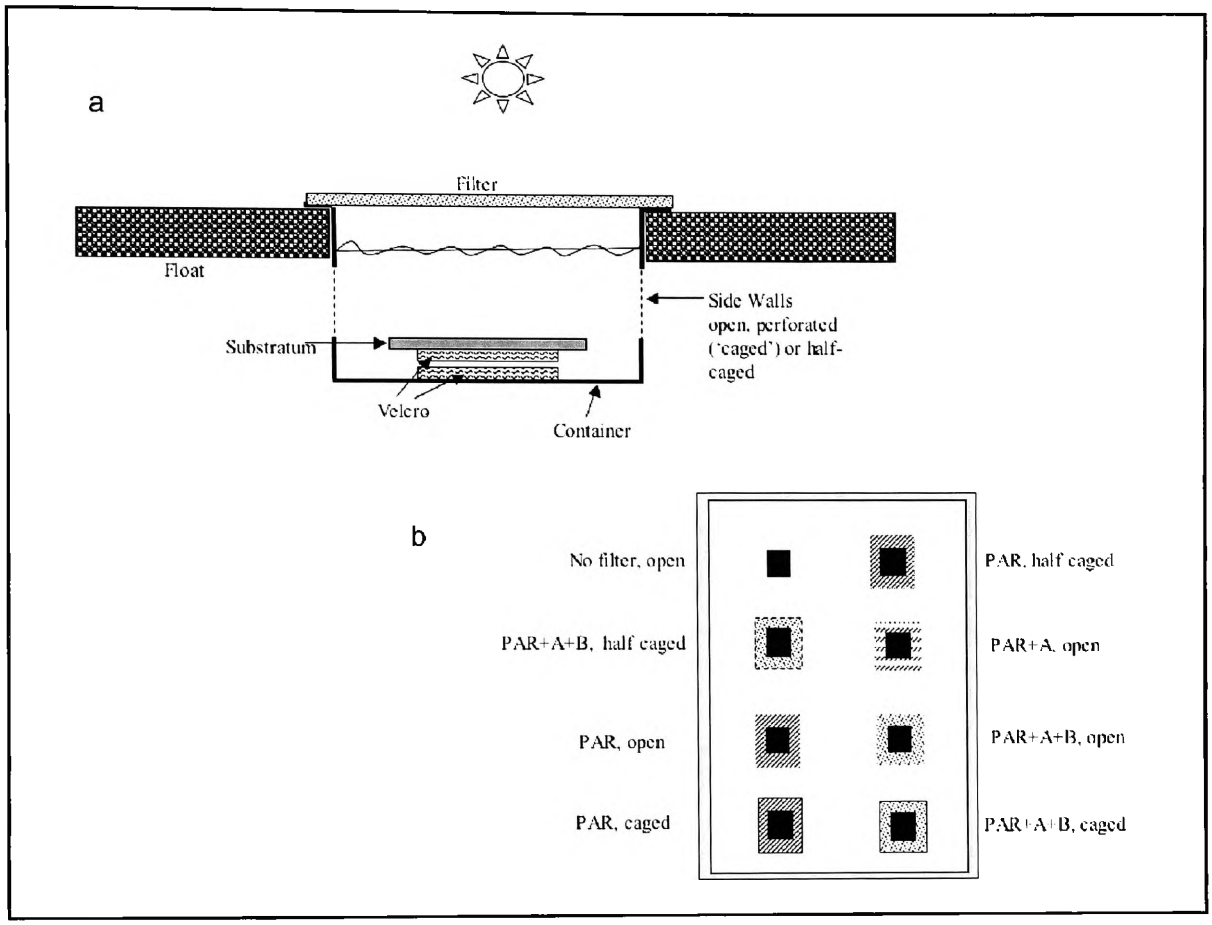

Figure 5. Experimental setup. (a) Side-view of one experimental unit. The distance between water surface and settlement substratum is 40 mm. (b) Block arrangement of single replicates of each of the 8 treatment combinations. In total 6 blocks (= 6 replicates) were deployed. Open: all walls provided with windows to allow consumer access. Perforated: walls perforated by numerous small holes to exclude local grazers. Half-caged: 1 wall with window, 3 walls perforated (cage control).

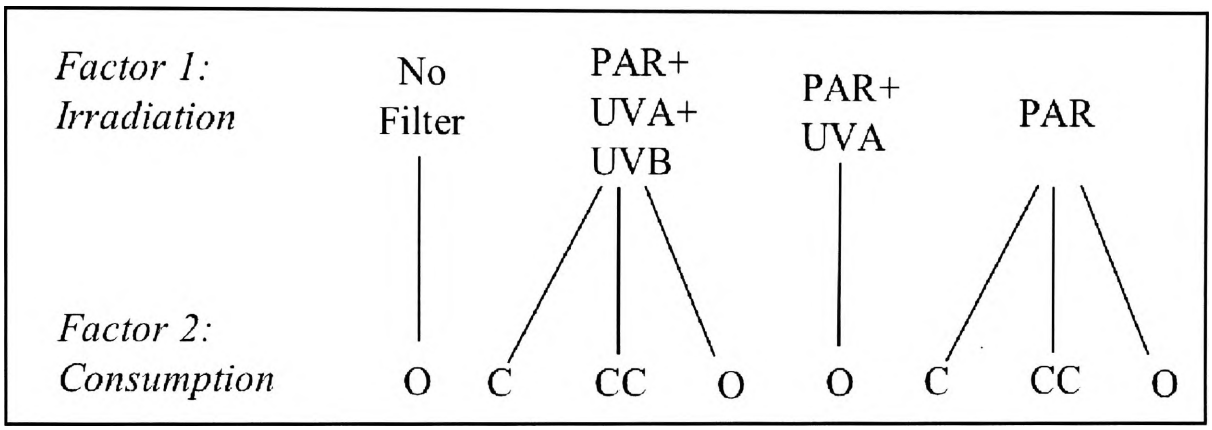

Figure 6. Factorial design. PAR + UVA + UVB, PAR + UVA, PAR = irradiation spectra reaching the settlement panels. O = open container (consumer access), CC = cage control (consumer access), C = cage (perforated container, no consumer access).

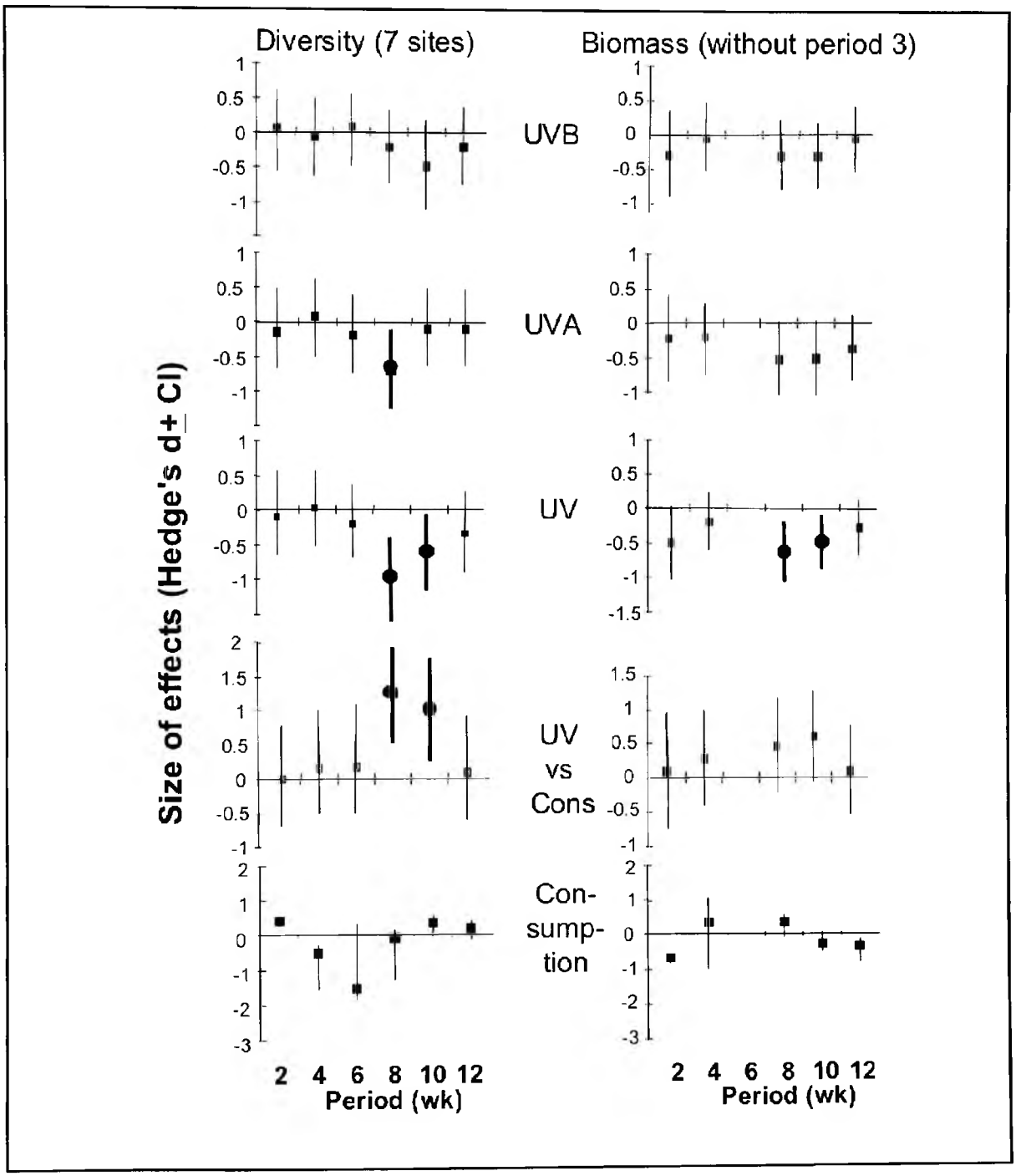

Figure 7. Results of UV and consumer impacts with reduced data set to obtain to homogeneity of variances. Diversity effects (left column): three most poleward sites (Norway, Antarctica, Germany) omitted. Biomass effects (right column: 6th week omitted.

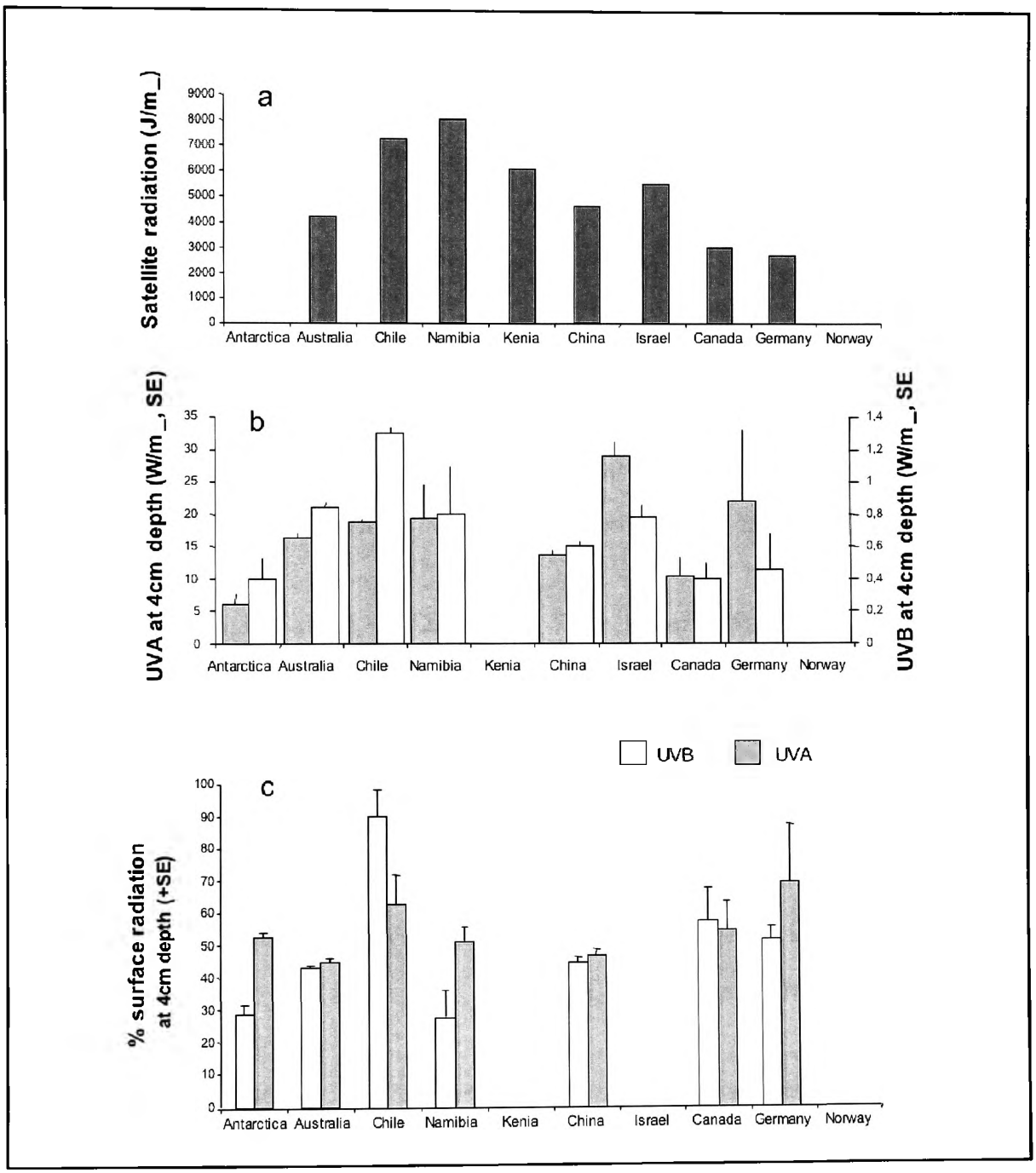

Figure 8. UV irradiation regime averaged over the experimental phase at each site. a: TOMS data for daily UVB doses. b: UVA and UVB irradiation around noon at 4cm depth (immersion depth of the experimental units). c: Reduction of UVA and UVB in the upper 4 cm water column by reflection, absorption and diffusion (% of incident irradiance). Missing values: deficient instruments.

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Acknowledgments

We gratefully acknowledge financial support by GTZ Proklima, Namibia & Germany. The University of Namibia and BENEFIT, Namibia, generously provided submersible UV meters. Contribution of co-authors: Regional experiments were carried out by AD & JK in Antarctica, SD in China, STD in Australia, JJ in Norway, DK in Kenya, HKL& BW in Canada, MM in Namibia and Germany, MT & ML in Chile, DZ in Israel. MM, JT & BW contributed substantially to the comparative analysis. Concept and coordination of the project by MW.

Correspondence and requests for materials should be addressed to M.W. (mwahl@ifm.uni-kiel.de).